# Biotic analogies for self-organising cities

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## Introduction

Nature has inspired urban designers since they first attempted to understand the complex functional order of cities. Cities have been seen as organisms (Mumford, 1938; 1961) or ecosystems (Girard, 2014; Marshall, 2009); comprising components analogous with cells, tissues, organs, flesh, blood, tentacles and skeletons (Le Corbusier, 1947; Mumford, 1938; Soria y Mata, 1998); and subject to urban growth, morphogenesis, metabolism, adaptation and evolution (Geddes, 1915; Marshall, 2009; Rogers, 1998). Mining of other disciplines for inspiration and describing phenomena using analogies, metaphors and similes has advanced understanding of urban problems and investigation of possible solutions, as seen in the proliferation of biomimicry solutions for designing more sustainable cities (Benyus, 2009), evacuation routes (Dias et al., 2013), and new building materials (Vogel, 1998).

However, amid the profusion of biological comparisons it remains unclear whether or not usage is consistent or biologically robust. In these circumstances, biological analogies risk being dismissed as unscientific, or merely figures of speech, so opportunities for their advancement of understanding and application may be missed. As 'nature-based solutions' and scientific approaches to urbanism (Batty, 2012; Marshall, 2012) gain increasing attention, drawing inspiration from appropriate models (Batty, 2007; Moroni, 2015), analogies (Steadman, 2008), and metaphors (Chettiparamb, 2006; Tippett, 2010), it is an opportune time to revisit the nature of biological analogies in a systematic way.

This overall mission would imply an extensive research agenda, potentially tracking relationships between biological and urban phenomena on multiple fronts, including several processes such as self-organisation, metabolism, adaptation and evolution. As a first step, this paper addresses self-organisation.

Self-organisation refers to a bottom-up process where pattern emerges from numerous interactions among the components of an initially unpatterned system. Self-organisation does not require sentience of the self-organising units or an external agent. Rather, pattern emerges through local interactions between the system's components using positive and negative feedback.

Self-organisation research occurs across the natural and physical sciences, and urban researchers have drawn upon these to inspire bottom-up approaches to generating urban order (Batty, 1998; Portugali, 1997). It is an inherently cross-disciplinary domain, routinely recognised as having both biological and non-biological manifestations, with direct operational equivalences that go beyond the figurative. Consequently, our treatment of self-organisation provides a lens through which to study phenomena spanning the biological and the urban, offering a model for future application to other areas where biology has influenced urban design including development, adaptation, and evolution.

Here, our aims are to (i) identify a set of analogies, metaphors and similes based on self-organisation that are used in urban design; (ii) for analogies, establish a method for assessing their clarity, depth, and application to urban design; (iii) assess the validity of analogies according to contemporary biology; (iv) explore how these analogies link up or relate to each other in a more systematic way; and hence (v) establish a framework which contains and expresses the observed urban/biological relationships, and may also be used to generate new ones. We believe that this is a potentially pioneering agenda, generating a method that could find further application in other contexts, and wherein the scrutiny from contemporary biology is itself novel, yielding insights that are correspondingly original.

First, we briefly introduce the history of self-organisation and its current use in urban design and biology. Secondly, we undertake a systematic analysis of analogy between urban and biological disciplines, quantifying the use of analogy, and their biological validity. Finally, we suggest a new biotic framework through which to interpret the analogical space, locating existing analogies in relation to each other and helping to stimulate new analogies for urban application.

**Self-Organisation**

Whilst the idea that order can emerge by itself dates back to Democritus and Lucretius, it was Emmanual Kant who first coined the term 'self-organisation' arguing that organised beings can be distinguished from non-living entities because they have a self-organising 'formative power' which propagates itself that required a new type of science to explain it, because neither physics nor chemistry could (Karsenti, 2008; Keller, 2008).

A major challenge was that biology is largely based on chemical and biochemical reactions which don't self-organise (Tabony, 2006). Lotka (1909; 1925) submitted that chemical reactions might self-organise into oscillating chemical systems, akin to predator-prey population size dynamics, later confirmed experimentally by Belousov (1951) and Zhabotinsky (1964) and mathematically by Turing (1952). Interest proliferated across fields, leading to new understanding of the thermodynamic properties of dissipative systems (Prigogine and Nicolis, 1967), cybernetics and feedback (Ashby, 1960; Wiener, 1948), synergetics (Haken, 1977), fractals (Mandelbrot, 1982) etc. Such studies ushered in a new era in self-organisation research where both the animate and inanimate were products of self-organisation in nonlinear, far-from-equilibrium, open systems, and their results have been applied across the social, computational, economic, physical and biological sciences (Keller, 2009).

In biology, Goldbeter and Lefever (1972) used Belousov-like equations to describe glycolytic oscillations, and Turing's work has been applied to pattern formation in mammals' coats (Murray, 1988), and embryogenesis (Glover et al., 2017). Today, self-organisation research spans all levels of biological complexity, from micro: formation of the first polymers (Freire, 2015) and cell division (Karsenti, 2008); to macro: schooling fish (Camazine et al., 2001), species distributions (Alados et al., 2007), ecosystems (Lenton et al., 2018).

Urbanists also adopted self-organisation from the physical sciences. Prigogine's theory of dissipative systems was applied to the appearance of central places (Allen et al., 1985). Portugali (Haken and Portugali, 1996; Portugali, 1997) introduced synergetics, Batty and Xie (1997) pioneered cellular automata techniques, and both applied fractal and synergetic approaches to chaos theory (Batty and Longley, 1994; Portugali, 1997). Today, self-organisation is routinely considered a central process in urban development (Yamu and Frankhauser, 2015) yielding important insights for urban planners considering topics including: urban intensification (Janssen-Jansen, 2013), urban codes (Moroni, 2015) and self-governance (Rauws and de Roo, 2016); for a recent mapping of research see de Bruijn and Gerrits (2018).

As biology has drawn from the physical sciences, urban designers are applying biological self-organisation to urban environments. Indeed, the richest potential for understanding urban self-organisation would appear to lie in learning from biology, which exhibits the fullest range of self-organising phenomena, from inanimate biomolecules through the animate world of sentient beings to ecosystems and Gaia. As such, a key challenge is to clarify how the biological component of self-organisation is being related to urban processes and where further insights might be found.

## Methods

To examine how biological inspiration is being used within studies of urban self-organisation we identified all articles referencing self-organisation between 2000-2016 in five urban design and five biology journals, resulting in 69 urban design and 205 biological articles. We listed 25 biological terms (Fig.1) and recorded their frequency per paper. Biology-inspired similes, metaphors and analogies were identified in the urban literature, and analogies were assessed for clarity, depth, biological soundness, and applicability using a 1 to 5 scale (1=low, 5=high). We used mapping analyses and boxplots to compare term usage between disciplines, and Sankey diagrams and 3D-scatterplots to assess how analogies were employed. For a fuller version of the methods and results see SM1.

## Results

The number of urban articles referring to self-organisation increased overall between 2000-2016 (SM2), and covered a wide range of urban design topics (SM3) including mechanistic models, unplanned local initiatives, and the planning process.

### *Biological Terms*

All urban papers contained at least one of our biological terms other than self-organisation. Mapping of terms revealed inconsistencies in connections between the two disciplines (Fig.1) highlighting differences in the way the terms are used (SM4).

[Fig.1]

In both disciplines the closest links were between 'self-organisation' and 'evolution'. 'Adaptation' and 'ecology' are also closely connected, after which, the two disciplines diverge. The biological mapping stressing the importance of 'gene', 'mutation', 'natural selection', 'organism', and 'morphology', the urban mapping highlighting 'morphology', 'feedback', 'multilevel', and 'organism' (Fig.1).

Herein lies a key difference between the biological and urban realms. The biological mapping points to biology's central theorem: that an organism's adaptive traits are the product of evolution through natural selection and mutation is one mechanism of introducing genetic variation. Direct analogues of biological evolution are largely absent in urban planning (Mehmood, 2010), because those that do so face significant challenges including: defining urban genes and fitness, characterising urban gene to phenotype translation, identifying the units of survival and reproduction.

*Biological Comparisons*

Through further review of the urban articles 66 biological terms were identified, which were used 2371 times. Biological terms were most often used *without* consciously invoking a biological comparison; despite this, 31.88% of urban articles contained a biological comparison: 15.94% analogy, 23.18% metaphor, 7.25% similes (The sum is more than 31.88% as some papers contained more than one kind of biological comparison. SM3)

Thirteen analogies were identified, in eleven papers. 69.23% of which were made between different hierarchical levels e.g. city–organism is cross-level analogy, person–organism is a direct-level analogy (Fig.2). 38.46% of the analogies related directly to self-organisation. Analogies were often found to be either unclear (mean=2, s.d.=1), and/or, of limited depth (mean=2.15, s.d.=1.07); whilst depth of analogy showed no connection with urban applicability we found a positive association between the depth, and to a lesser extent the clarity, of an analogy and its biological soundness (SM5). Applicability was found to be higher when an analogue was both clearly conveyed and the biological content was accurate (SM5).

[Fig.2]

**Nature-Inspired Urbanism?**

*Depth, Clarity, Biological Soundness*

Overall, the analogies lacked depth and clarity. Lack of depth had nominal effect on the applicability of an analogy to the urban realm. Rather, the more reliable the biological basis, and the more clearly the information was applied, the better the fit of the biological analogue. As depth and clarity increased, the biological information was found to be more dependable, a not wholly surprising result as clarity and depth are both qualities required to adequately assess biological content.

That an analogy was not required to be deep to be successful is more interesting. An analogy may be so commonly employed that in-depth interrogation is not required to impart meaning e.g. city is organism. The purpose of the analogy may not call for an in-depth analysis of biological theory. Or, the biological connection may not be particularly important to the author, who instead could opt for deeper analogies with other disciplines, which may themselves be analogous, and produce similar insights (Helbing et al., 2001).

Concerningly a lack of depth and/or clarity can make it difficult to distinguish the type of biological comparison being used, leaving readers to infer meaning according to their own biases. For example, depending on the author, and reader, city as organism may be purely symbolic (Nientied, 2016), or an analogy from which logical arguments can be extended and planning decisions made (Golubiewski, 2012). Combine this with terms having multiple definitions or context sensitivity and it is easy to see how confusion may occur.

All of these are common problems facing writers who use comparative language to express ideas (Chettiparamb, 2006). However, with over half of the world's population inhabiting cities and increasing disconnection from the natural environment (Cox et al., 2017), urban authors face a more fundamental problem when using biological comparisons: that of using the unfamiliar to describe the familiar.

Urban DNA is a particularly interesting example (Boelens, 2014; Nientied, 2016; Wu and Silva, 2011). Whilst DNA is a part of us, it is not a part we see or feel, or identified the role of until Avery et al. (1944). Thanks to the efficacy of language, art, and the fundamental desire to understand the nature of being, DNA has become relatable. Its structure, the information it inscribes and 'mystical powers' have been described as a twisted ladder, a blueprint, an immortal spiral (Rovira, 2008).

The particular comparisons employed can markedly alter our understanding, and the implications, of a concept. Informational and essentialist DNA metaphors have shaped our laws (Silvestro, 2016), and metaphors regarding DNA's components have shaped research trajectories (Avise, 2001). New findings may invalidate descriptors, eliciting calls for their alteration or discontinuation e.g. 'DNA is a blueprint' lost favour because it implies a direct mapping of genetic information to phenotype, when in actuality, the same genetic code can produce remarkably different phenotypes e.g. queen and worker honeybees. Perhaps 'genetic code' remains in good standing because 'code' does not suggest decryption method, allowing many final forms and the capacity to integrate new research findings. As such, the analogy of urban DNA might better be conceptualised as a set of generative codes, or framework rules, resulting in a self-organised urban order, as opposed to urban order generated by a blueprint.

Ultimately, research requires the clear communication of ideas, so they can be assessed and discussed. Where confusion occurs advancement is hampered (Steadman, 2008). Defining terms and the limits of one's analogies can help reduce confusion, clarify thinking, and elucidate when a field where inspiration is being drawn from is itself using the same term in different ways. For example, in biology, terms such as metabolism are regularly used across disciplines and hierarchical levels but refer to different processes (Golubiewski, 2012). Thus, referring to the city as ecosystem and as organism, particularly in the same paper, can have very different implications, muddling the narrative.



*Description, Inspiration, and Mechanism*

Analogies were used to either describe, inspire or suggest mechanism. In description, the opportunity for an extended metaphor to be confused for analogy was highest. For example, is Frenkel's (2004) description of cities as '*multistructural organisms as reflected in the spectrum of their functions*' and use of taxonomic methods to '*classify cities according to their characteristics*' a metaphor, or an obvious extension to the commonly expressed analogy?

Inspirational analogies encouraged new ways of thinking about the urban environment. Salingaros (2010) used the earliest bio-molecules to inspire urbanists to look beyond an urban element's primary function to consider secondary and potential catalytic effects. Finally, mechanistic analogies such as Barker (2012) and Adamatzky et al. (2017) who employed different slime mould species to reveal how simple, local, bottom-up interactions lead to urban formation and efficient transport networks, respectively.

Three of the five analogies that proposed mechanism were directly related to self-organisation. Of course, as self-organisation is a mechanism this correlation is unsurprising. More interesting is that two of these three studies drew comparisons of urban systems from the behaviour of slime moulds, which, over recent years, have helped overturn notions of the minimum level of intelligence needed to solve complex problems, leading to the development of simpler algorithms to solve modern day human problems.

Difficulties arise in that: models have mostly been deductive rather than predictive, limiting their current value to urban planning (Adamatzky et al., 2017); the focus on economic 'rationality' can favour highly productive regions rather than the growth of underdeveloped regions (Vanoutrive et al., 2016); the spatial scale and morphology of slime mould experiments may dramatically change the solutions arrived at and might not always be optimal (Reid et al., 2012), as slime moulds can make irrational decisions, similar to humans (Latty and Beekman, 2010).

Examining a variety of organisms may be more informative to urban planners, providing a variety of solutions to choose from. For example, Argentine ant (*Linepithema humile*) networks prioritise cost and efficiency over robustness (Cabanes et al., 2014), the fungus *Phanerochaete velutina*'s networks maximise robustness and efficiency (Bebber et al., 2007), whilst the networks of wild polydomous ant colonies, which can stretch thousands of kilometres, have more connections than those found in lab populations, suggesting robustness may be a more important factor in ecologically valid situations (Cook et al., 2014).

*Analogies Across Levels of Scale*

Both biological and urban systems are characterised by nested levels of increasing complexity, where each level is primarily composed of the level below but possesses emergent properties not present in that level. Mechanisms leading to the spatial organisation of lower level entities forming higher hierarchical levels include self-organisation, environmental constraint, and cooperation (Maynard-Smith and Szathmáry, 1995; Takeuchi and Hogeweg, 2009)

Biological levels extend from molecules to Gaia, although authors generally define a narrower, question-appropriate range. The delineation between biological hierarchies is not as neat as it might initially appear. Single celled organisms, for example, inhabit both the cell and organismal levels, and an organism is a community, called the holobiont, when microbiome, virome and parasites are accounted for.

The urban realm can include human concepts of geographical/economical/political areas but, for most urban researchers their questions will fall between the people and regions levels, and like biological levels of organisation, delineation between urban levels and elements at different scales is not always clear cut (Alexander et al., 1977; Kropf, 2014). Actually, the urban hierarchy is nested within the biological hierarchy. People are organisms so are found on the biological hierarchy at the level of organism. The urban environment is a type of ecosystem; however, it can also be considered at lower hierarchical levels (e.g. community), depending on the question being asked.

Most of the analogies we identified crossed hierarchical levels (Fig.2), analogising city to organism, land uses to genes, and pedestrian paths to capillaries. Analogies existing at equivalent hierarchical levels included city as ecosystem and models derived from slime moulds because, whilst a slime mould and transport network (for example) may not immediately appear to be at the same hierarchical level, the rules for their formation are both generated at the organismal level, for modern human transport networks are often founded atop the informal, emergent trails of our ancestors.

Logically, all analogies that operate below the level of the organism must be cross-level analogies. However, an interesting anomaly may occur with plan/blueprint/design as urban ‘genotype’. A plan/design is neither nested within nor essential for the construction or functioning of higher-level entities. Indeed, it may merely be a representation of a completed form, rather than its generator. What is nested within and essential to the construction and functioning of urban form is the urban population, each with genomes, and so, one could postulate that *people* are the urban genotype.

Employing evolutionary analogy Silva (2016) states that tactical urbanism (a self-organised approach that transform the urban environment through self-built interventions) provides the ‘energy’ for urban evolution, implying ‘energy’ translates to mutation. However, tactical urbanism can be more clearly and instructively described in terms of niche construction where, rather than city as organism it is analogous to a hive, burrow etc.

Niche construction theory is a broadening of Dawkins' (1982) extended phenotype hypothesis such that any manipulation of the environment by the organisms inhabiting it, and the effects of those manipulations on adaptive fitness of the organism, its progeny and other organisms in the environment, are now included (Odling-Smee et al., 2003).

Niche construction theory recognises that by altering their environments organisms alter the selection pressures acting upon them, such that the organism adapts to the environment *and* the environment adapts to the organism. Thus, the organism produces an ecological inheritance (Odling-Smee et al., 2003) which, if fitness enhancing, will promote co-evolution of trait and constructed niche. In social groups, cultural inheritance can also drive niche construction (Ellis, 2015; Kendal et al., 2011).

Theoretical examinations integrating ecological and cultural inheritances have found that niche construction is capable of overriding, reversing or accelerating natural selection, and of generating unusual population dynamics (Laland and Brown, 2006; Laland et al., 2001). Further, gene-culture-co-evolution has been proposed as the dominant mechanism of adaptation in humans (Ellis, 2015; Laland et al., 2010). Therefore, the creation of the human built environment is not only part of urban evolution, it is a part of human evolution, past and present. In other words, '*we co-evolve with the environment we create*' (Kropf, 2017).

It is often self-organisation, operating amongst individuals or across environmental components, that shapes constructed niches. Social insects build nests, orders of magnitude larger than an individual through self-organised collective action, following cues derived internally, from nestmates, or environmentally (Green et al., 2017). Architecture has produced buildings inspired by social insect nests but none has captured the adaptive quality of nest architecture, where structure and function have become one, and mechanism is derived through a desire to maintain a stable internal environment that can be cognitively and physiologically produced (Penn and Turner, 2018; Turner and Soar, 2010).

Returning to the example of tactical urbanism: as in niche construction theory, tactical urbanism denotes a self-organised, bottom-up approach, that transforms the urban environment, through self-built interventions (Silva, 2016), rather than being a mutation in an organism. Tactical urbanism initiatives include 'Guerrilla Gardening', 'Intersection Repair', 'Pop-up Cafes'. Their role seems often to beautify and connect, and these homeostatic desires could be routed in a physiologically evolved need to reduce stress. When possible, portions of the urban population may be intuitively transforming their environments, removing or reducing aspects that negatively impact fitness. In doing so, they not only enhance their own fitness but that of their neighbours, increasing the probability of accruing benefits through reciprocal altruism or kin selected benefits. The fitness enhancement may, today, be small, but for the urban planner, the lessons may be of use. Firstly, such initiatives are likely excellent venues of inspiration for positive design ideas that can be extended more widely. Thus, allowing space for citizen-led, self-organised, bottom-up approaches to exist is of great import. Secondly, urban planners could co-opt this mechanism by identifying ways to translate innate homeostatic preferences into urban design, enabling the urban population to alter their environments for public good by building environmental feedback mechanisms into architecture (Pasquero and Zaroukas, 2016).

**Analogical Space to Biotic Framework**

Our analysis revealed a preponderance of cross-level comparisons over equivalences (direct-level analogies). Indeed, even when a level of equivalence was being evoked it was often masked. Barker (2012), for instance, modelled how land-use decisions generate cities, where the model and decision rules were inspired by self-organised slime mould agglomerations. That the land-use decisions are made by humans and the model is using slime mould behaviour to propose simple rules underpinning human behaviour, is not explicitly stated. Operating so, the urban literature risks overlooking key areas of instructive insights that fall at the level of equivalence.



In biology, evidence accrues through analogous research across taxa, where different evolutionary and life histories lead to different predictions drawn from the same theory. In feeding into these bodies of literature direct-level analogies (equivalences) could provide a more substantial contribution to urban researchers than the purely figurative. For, after all, humans are organisms too.

To demonstrate our thinking we propose the biotic framework (Fig.3) – so named because it emphasises that both organisms and their constructed environments are biotic - relating to or resulting from living organisms. In a very literal sense, our cities, indeed all human environmental modifications, are biotic. Our emphasis on the biotic is in contradistinction to traditional emphases on human versus nature, or organic versus inorganic – though both of these form part of the framework.

[Fig.3]

The framework provides a rationale for locating and identifying analogies, particularly those where the processes operating are most likely to be comparable to urban processes, and encourages awareness of the entire system. We present two versions of the biotic framework (a) presenting the framework and its dimensions, (b) showing a subset of the biological comparisons identified in the reviewed literature (green solid lines), some well-known comparisons that not present in the reviewed literature (orange dashed lines), and some connections that we suggest could provide new inspiration for urban designers (grey dashed lines) (Fig.3).

Protruding into the foreground are the lower hierarchical levels. At the front are biomolecules and compounds which form the basis of life, composing every living organism, prompting 'the continuity thesis' which suggests that there is no break between physiochemical and biological systems (Freire, 2015). The coalescence of molecules forms the constituent parts of cells, which come together to form tissues, organs, and organism.

Biological comparisons between urban elements and levels below that of organism have proved popular, inspiring new conceptions of urban environments and processes. Comparisons made between molecules (Salingaros, 2010), or parts of an organism (Furtado et al., 2012; Mehaffy et al., 2010; Salingaros, 2010), and the urban environment are, by definition, cross-level analogies. Whilst there is no denying the merits of such comparisons, we propose that, where an analogy relates to process, inspiration will more readily be found and likely better fit the example, when it is drawn at the level of equivalence.

The level of the organism is the first hierarchical level where drawing upon equivalence is possible. Here, the living entity, be it human, slime mould, ant, or bower bird, is the focus.

Its cognition, behaviour, and decision making, are of primary importance because such rules determine how organisms use, move around and understand the environment, and population distributions. At this level, natural and cultural selection play dominant roles in shaping the behavioural rules and physiological requirements of the organism.

Moving into the diagram from the position of the organism, two planes run parallel, the lower signifying increasingly large clusterings of the same organism (group, population, species), the upper signifying the organism's constructed environment. We adopt the definition from niche construction theory to characterise a constructed environment - any modification of the environment by an organism which alters the selective pressures acting upon it and other organisms inhabiting that environment. As such, constructed niches vary dramatically between organisms including leaf litterfall (Bigelow and Canham, 2015), birdsong repertoire size (Creanza et al., 2015), and termite mega-structures (Turner, 2004). The two planes run parallel because to differing extents the constructed niche will impact the selective pressures acting on those groupings.

To represent hierarchical relationships between elements within the human built environment we build upon a representation proposed by (Kropf, 2014), adding neighbourhood, city and conurbation as familiar reference points, although these do not imply an exact structural continuation of the lower levels.

Humans, like all organisms, don't inhabit the world alone or immune from the effects of the environment. When organisms interact they form communities; the combination of communities and physical processes are ecosystems, which in turn combine to biomes and eventually Gaia. At these levels, natural selection plays a muted role. Rather, system evolution and adaptation may be guided by self-organised mechanisms (Lenton et al., 2018). The urban environment is an ecosystem and so, analogies drawn between mechanisms of natural ecosystem functioning, resilience, evolution, adaptation etc., with urban processes are examples of equivalences.

As each hierarchical level is an emergent property from coalescence of the level below, disturbance at one level can trigger changes upwards and downwards. The biotic framework draws attention to the interconnected and hierarchical nature of the whole system and can be used to interrogate the implications of transformations across hierarchical levels. Analogy does not have to include multiple hierarchical levels to be of use. However, by considering the implications of an analogy across multiple hierarchical levels, and defining the limits of the analogy, not only are the clarity and biological soundness likely to be improved (a key indicator of the fit of an analogy to the urban realm) but the potential to identify novel insights is markedly increased.

Indeed, the framework motivated us to propose, for demonstrative purposes, three new comparisons, that might serve to inspire urban design and the rules that formulate urban environments (Fig 3). Firstly, we refer back to transport networks and the observation, from lab and field experiments with ants and slime moulds, that outcomes of self-organisation are highly dependent on environmental variables, and that looking at a variety of organisms how they respond to environmental variability will be most instructive to urban planners when determining similar situations and trade-offs. Secondly, as initiatives work to bring food production into our urban environments (Whittinghill and Rowe, 2011) using natural communities to inspire our understanding of the needs of urban communities will become ever more crucial. A classic example of farming in animal societies is that of fungus farming ants; this turns out to be a multi-species mutualism (Barke et al., 2010) highlighting the need to consider community dynamics even within complex constructed niches, and the role of the constructed niche in shaping those communities and dynamics. Thirdly, we propose that epigenetic mechanisms for pattern formation (non-genetic influences on gene expression that affect traits such as coat pattern, caste differentiation, and that allow organisms to rapidly respond to changing environments) could inspire a new (or newly recognised) layer of 'epigenetic' directions within urban design/planning. Such an epigenetic layer would guide where and when different codes or framework rules are deployed, and could include 'rules for the production of rules for the activation of processes' (Moroni, 2015), integrated with 'location-specific development regulations, traditionally expressed in the land-use plan, with generic regulations' (Rauws and de Roo, 2016). In other words, identifying and deploying the urban equivalent of epigenetic mechanisms could help guide self-organising urbanism in a third way that offers a balance between more purely bottom-up or top down processes.

## Conclusion

Our research has found a rich diversity of biological analogies associated with urban phenomena relating to self-organisation but these are currently applied with limited depth and relation to each other. Still, they could be applied more deeply and systematically, and we show how via the biotic framework, which has also stimulated new analogies. We believe this analysis breaks new ground – perhaps most significantly bringing fresh biological insight and scrutiny into this territory since the time of Patrick Geddes – and can pave the way for further research agendas, including application to other analogical processes (e.g. urban adaptation, evolution) and other disciplinary domains.

In our analysis we found that analogies between biological and urban realms were drawn from molecule to ecosystem and human to city. They mostly crossed hierarchical levels and the potential for confusion from the complexity of these different relationships led us to generate the biotic framework (Fig.3). This framework was initially created to articulate the analogical space that has been the focus of this paper, but in doing so provides a structure for conceptualising and interpreting relationships between key domains of the biotic sphere.

Our analysis suggests that attention could be usefully directed to the more direct analogies or equivalences because: (i) cities are actually ecosystems; (ii) our built environments are actually constructed niches; (iii) our built environments have a material effect on our species' actual ongoing evolution. Furthermore, these three statements are linked and can be made more visually explicit via the biotic perspective. In addressing equivalence, insights from reading across human and natural realms may be particularly pertinent because they access overarching theories, built on evidence from a wide array of organisms, to explain and describe the evolution and mechanistic underpinnings of the phenomena.



For the urban environment, comparisons operating at the level of the organism and providing feedback between organism and environment will be particularly pertinent. Niche construction theory has already been applied to human evolution (Laland and Brown, 2006; Laland et al., 2001; 2010) and combining biological theory e.g. optimal foraging or cultural niche construction, with insights from past trends, could help identify planning perspectives that are adaptive, resilient, commensurate with our inherent desires for physiological comfort, and advance theory.

At higher ecological levels, the environmental effect of humans is ever more tangible. Calls to circularise our systems (Williams, 2019), or mimic the services provided by natural ecosystems (Benyus, 2009) do not benefit from the view of city as organism; rather, the view of cities as ecosystems, and drawing inspiration from natural ecosystem functioning, failures and resilience, provides a stronger basis from which to construct solutions to the ultimate problems facing future urban environments. As such, choosing the right analogy is not purely a choice of literary expression but, as with the example of DNA, can make a material difference to our perception of a problem and hence appropriate solutions.



Interestingly, the biotic framework can be seen as a freshly explicit expression of Geddes's understanding of the equivalence of the human and natural realms, that has more often remained implicit (Geddes, 1915). His assertions regarding the interaction between human evolution and environment invoke modern niche construction theory, his concept that cooperation overrides conflict is supported by multilevel selection theory. As biology furthers its understanding of evolutionary processes, self-organisation is emerging as a principal force, shaping form through the self-organised behaviours of organisms, and ecosystems through self-organising mechanisms far removed from the reach of the genes. This could provide an area for future application linking *urban* self-organisation and evolution, wherein generative codes or framework rules could play a fitting part in future urbanism. Overall, analogies at the level of equivalence could become of increasing interest, even to those wary of organicist metaphors, not despite their biological roots but because through them comparison can go beyond the purely figurative.

**References**

Adamatzky A, Allard O, Jones J, Armstrong R. (2017). Evaluation of French motorway network in relation to slime mould transport networks. *Environment and Planning B.* **44**(2):364–383

Alados C, Aich A, Komac B, Pueyo Y, García-Gonzalez R. (2007). Self-organized spatial patterns of vegetation in alpine grasslands. *Ecological Modelling.* **201**(2):233–242

Alexander C, Ishikawa S, Silverstein M, Jacobson M, Fiksdahl-King I, Angel S. (1977). *A pattern language: Towns, buildings and construction*. Oxford University Press, New York

Allen P, Sanglier M, Engelen G, Boon F. (1985). Towards a new synthesis in the modeling of evolving complex systems. *Environment and Planning B.* **12**(1):65–84

Ashby W. (1960). *Design for a Brain: the origin of adaptive behaviour.* Wiley, New York

Avery O, MacLeod C, McCarty M. (1944). Studies on the chemical nature of the substance inducing transformation of pneumococcal types. *Journal of Experimental Medicine.* **79**(2):137–158

Avise J. (2001). Evolving Genomic Metaphors: A New Look at the Language of DNA. *Science.* **294**:86-88

Barke J, Seipke R, Grüschow S, Heavens D, Drou N, Bibb M, Goss R, Yu D, Hutchings M. (2010). A mixed community of actinomycetes produce multiple antibiotics for the fungus farming ant *Acromyrmex octospinosus*. *BMC Biology.* **8**:109

Barker D. (2012). Slime Mold Cities. *Environment and Planning B.* **39**(2):262–286

Batty M. (1998). Urban Evolution on the Desktop: Simulation with the Use of Extended Cellular Automata. *Environment and Planning A.* **30**(11):1943–1967

Batty M. (2007). *Cities and Complexity: understanding cities with cellular automata, agent-based models, and fractals.* MIT Press, Cambridge (MA).

Batty M. (2012). Building a science of cities. *Cities.* **29**:S9–S16

Batty M, Longley P. (1994). *Fractal Cities: a geometry of form and function*. Academic Press, New York.

Batty M, Xie Y. (1997). Possible urban automata. *Environment and Planning B.* **24**:175–192

Bebber D, Hynes J, Darrah P, Boddy L, Fricker M. (2007). Biological solutions to transport network design. *Proceedings of the Royal Society B.* **274**(1623):2307–2315

Belousov B. (1951). *A periodic chemical reaction and its mechanism. Oscillations and travelling waves in chemical systems.* Wiley, New York.

Bennett J, Cooper M, Hunter M, Jardine L. (2003). *London's Leonardo: the life and work of Robert Hooke*. Oxford University Press, Oxford

Benyus J. (2009). Biomimicry in action. https://www.ted.com/talks/janine_benyus_biomimicry_in_action

Bigelow S, Canham C. (2015). Litterfall as a niche construction process in a northern hardwood forest. *Ecosphere.* **6**(7):117–14

Boelens L. (2014). Delta Governance: The DNA of a Specific Kind of Urbanization. *Built Environment.* **40**(2):169–183

Cabanes G, van Wilgenburg E, Beekman M, Latty T. (2014). Ants build transportation networks that optimize cost and efficiency at the expense of robustness. *Behavioral Ecology.* **26**(1):223–231

Camazine S, Deneubourg J-L, Franks N, Sneyd J, Bonabeau E, Theraula G. (2001). *Self-organization in biological systems.* Princeton University Press, Princeton.

Cook Z, Franks D, Robinson E. (2014). Efficiency and robustness of ant colony transportation networks. *Behavioral Ecology and Sociobiology.* **68**(3):509–517

Cox D, Hudson H, Shanahan D, Fuller R, Gaston K. (2017). The rarity of direct experiences of nature in an urban population. *Landscape and Urban Planning.* **160**:79–84

Creanza N, Fogarty L, Feldman M. (2015). Cultural niche construction of repertoire size and learning strategies in songbirds. *Evolutionary Ecology.* **30**(2):285–305

Dawkins R. (1982). *The Extended Phenotype*. Oxford University Press, Oxford

de Bruijn E, Gerrits L. (2018). Epistemic Communities in Urban Self-organization: A Systematic Review and Assessment. *Journal of Planning Literature.* **33**(3):310–328

Dias C, Sarvi M, Shiwakoti N, Ejtemai O, Burd M. (2013). Investigating collective escape behaviours in complex situations. *Safety Science.* **60**:87–94

Ellis E. (2015). Ecology in an antropogenic biosphere. *Ecological Monographs* **85**(3):287–331

Freire M. (2015). Nontemplate-driven polymers: clues to a minimal form of organization closure at the early stages of living systems. *Theory in Biosciences.* **134**(1-2):1–18

Frenkel A. (2004). Land-use patterns in the classification of cities: the Israeli case. *Environment and Planning B.* **31**:711–730

Furtado B, Ettema D, Ruiz R, Hurkens J, van Delden H. (2012). A cellular automata intraurban model with prices and income-differentiated actors. *Environment and Planning B.* **39**(5):897–924

Ganis M, Minnery J, Mateo-Babiano I. (2016). Planning people-places: A small world network paradigm for masterplanning with people in mind. *Environment and Planning B.* **43**(6):1075–1095

Geddes P. (1915). *Cities In Evolution.* Williams & Norgate, London

Girard L. (2014). Creative Initiatives in Small Cities Management: The Landscape as an Engine for Local Development. *Built Environment.* **40**(4):475–496

Glover J, Wells K, Matthäus F, Painter K, Ho W, Riddell J, Johansson J, Ford M, Jahoda C, Klika V, Mort R, Headon D. (2017). Hierarchical patterning modes orchestrate hair follicle morphogenesis. **15**(7):e2002117–31

Goldbeter A, Lefever R. (1972). Dissipative structures for an allosteric model: application to glycolytic oscillations. *Biophysical Journal.* **12**(10):1302–1315

Golubiewski N. (2012). Is There a Metabolism of an Urban Ecosystem? An Ecological Critique. *AMBIO.* **41**(7):751–764

Green B, Bardunias P, Turner J, Nagpal R, Werfel J. (2017). Excavation and aggregation as organizing factors in de novo construction by mound-building termites. *Proceedings of the Royal Society B.* **284**(1856):20162730–14

Haken H. (1977). *Synergetics: an introduction.* Springer, Berlin

Haken H, Portugali J. (1996). Synergetics, inter-representation networks and cognitive maps, in *The Construction of Cognitive Maps* Ed J Portugali. Springer Netherlands, Dordrecht

Helbing D, Farkas I, Molnar P, Bolay K. (2001). Self-organizing pedestrian movement. *Environment and Planning B.* **28**:361–383

Janssen-Jansen L. (2013). Delivering Urban Intensification Outcomes in a Context of Discontinuous Growth: Experiences from the Netherlands. *Built Environment* **39**(4):422–437

Karsenti E. (2008). Self-organization in cell biology: a brief history. *Nature Reviews Molecular Cell Biology.* **9**(3):255–262

Keller E. (2008). Organisms, Machines, and Thunderstorms: A History of Self-Organization, Part One. *Historical Studies in the Natural Sciences.* **38**(1):45–75

Keller E. (2009). Organisms, Machines, and Thunderstorms: A History of Self-Organization, Part Two. *Historical Studies in the Natural Sciences* **39**(1):1–31

Kendal J, Tehrani J, Odling-Smee F. (2011). Human niche construction in interdisciplinary focus. *Philosophical Transactions of the Royal Society B* **366**(1566):785–792

Kropf K. (2014). Ambiguity in the definition of built form. *Urban Morphology.* **18**(1):41–57

Kropf K. (2017). *The Handbook of Urban Morphology*. Wiley

Laland K. Brown G. (2006). Niche construction, human behavior, and the adaptive-lag hypothesis. *Evolutionary Anthropology.* **15**(3):95–104

Laland K, Odling-Smee F, Feldman M. (2001). Cultural niche construction and human evolution. *Journal of Evolutionary Biology.* **14**:22–33

Laland K, Odling-Smee F, Myles S. (2010). How culture shaped the human genome: bringing genetics and the human sciences together. *Nature Reviews Genetics.* **11**(2):137–148

Latty T, Beekman M. (2010). Food quality and the risk of light exposure affect patch-choice decisions in the slime mold *Physarum polycephalum*. *Ecology.* **91**(1):22–27

Le Corrbusier. (1947). *Concerning Town Planning*. The Architectural Press, London.

Lenton T, Daines S, Dyke J, Nicholson A, Wilkinson D, Williams H. (2018). Selection for Gaia across Multiple Scales. *Trends in Ecology & Evolution.* **33**(8):633–645

Lotka A. (1909). Contribution to the Theory of Periodic Reactions. *The Journal of Physical Chemistry.* **14**(3):271–274

Lotka A. (1925). *Elements of Physical Biology*. Williams and Wilkins, Baltimore

Mandelbrot B. (1982). *The fractal geometry of nature*. WH Freeman and Co, San Francisco

Marshall S. (2009). *Cities, design and evolution.* Routledge, Abingdon

Marshall S. (2012). Science, pseudo-science and urban design. *URBAN DESIGN International* **17**(4):257–271

Maynard-Smith J, Szathmáry E. (1995). *The Major Transitions in Evolution*. Freeman, Oxford

Mehaffy M, Porta S, Rofè Y, Salingaros N. (2010). Urban nuclei and the geometry of streets: The 'emergent neighborhoods' model. *URBAN DESIGN International.* **15**(1):22–46

Mehmood A. (2010). On the History and Potentials of Evolutionary Metaphors in Urban Planning. *Planning Theory.* **9**(1):63–87

Moroni S. (2015). Complexity and the inherent limits of explanation and prediction: Urban codes for self-organising cities. *Planning Theory* **14**(3):248–267

Mumford L. (1938). *The Culture of Cities.* Harcourt, Brace and World Inc, New York

Mumford L. (1961). *The City in History. Its Origins, Its Transformations, and Its Prospects.* Harcourt, Brace and Company, San Diego

Murray J. (1988). How the Leopard Gets Its Spots. *Science.* **246**:614–621

Nientied P. (2016). Metaphor and urban studies-a crossover, theory and a case study of SS Rotterdam. *City, Territory and Architecture.* **3**(1):1–10

Odling-Smee F, Laland K, Feldman M. (2003). *Niche Construction: The neglected process in evolution*. Princeton University Press, Princeton

Pasquero C, Zaroukas E. (2016). Design prototype. in *Research Based Education 2016*. The Bartlett School of Architecture, UCL, London

Penn A, Turner J. (2018). Can we identify general architectural principles that impact the collective behaviour of both human and animal systems? *Philosophical Transactions of the Royal Society B.* **373**(1753):20180253–12

Portugali J. (1997). Self-organizing cities. *Futures.* **29**(4-5):353–380

Prigogine I, Nicolis G. (1967). On symmetry-breaking instabilities in dissipative systems. *The Journal of Chemical Physics.* **46**:3542

Rauws W, de Roo G. (2016). Adaptive planning: Generating conditions for urban adaptability. Lessons from Dutch organic development strategies. *Environment and Planning B.* **43**(6):1052–1074

Reid C, Latty T, Dussutour A, Beekman M. (2012). Slime mold uses an externalized spatial 'memory' to navigate in complex environments. *Proceedings of the National Academy of Sciences.* **109**(43):17490–17494

Rogers R. (1998). The Evolution of London. in *Evolution, Society, Science and the Universe* Ed A Fabian. Cambridge University Press, Cambridge

Rovira S. (2008). Metaphors of DNA: a review of the popularisation processes. *Journal of Science Communication.* **7**(1):1–8

Salingaros N. (2010). Complexity and Urban Coherence. *Journal of Urban Design.* **5**(3):291–316

Sharpe W, Wallock L. (1987). *Visions of the Modern City*. Johns Hopkins University Press., Baltimore

Silva P. (2016). Tactical urbanism: Towards an evolutionary cities approach? *Environment and Planning B.* **43**(6):1040–1051

Silvestro I. (2016). A metaphorical history of DNA patents. *RIFL.* **2**:49–63

Soria y Mata A. (1998). The linear city. in *Selected Essays.* Eds R Le Gates and F Stour. Routledge/Thoemmels Press, London

Steadman P. (2008). *The Evolution of Designs: Biological analogy in architecture and the applied arts - a revised edition.* Routledge, Abingdon

Tabony J. (2006). Historical and conceptual background of self-organization by reactive processes. *Biology of the Cell.* **98**(10):589–602

Takeuchi N, Hogeweg P. (2009). Multilevel Selection in Models of Prebiotic Evolution II: A Direct Comparison of Compartmentalization and Spatial Self-Organization. *PLoS Computational Biology.* **5**(10):e1000542–17

Tippett J. (2010). Going beyond the metaphor of the machine: complexity and participatory ecological design. in *A planner's encounter with complexity* Eds G de Roo and E Silva Ashgate, Farnham, Surrey

Turing A. (1952). The Chemical Basis of Morphogenesis. *Philosophical Transactions of the Royal Society B.* **237**(641):1–37

Turner J. (2004). Extended Phenotypes and Extended Organisms. *Biology and Philosophy* **19**:327–352

Turner J, Soar R. (2010). Beyond Biomimicry: What Termites Can Tell Us About Realizing the Living Building in *Industrialised, Integrated, Intelligent Sustainable Construction*. I3CON

Vanoutrive T, Damme I, Block G. (2016). On the Rationality of Network Development: The case of the Belgian motorway network. *17th IPSH Conference, Delft* **3**:235-246.

Vogel S. (1998). *Cat's Paws and Catapults*. Norton and Company, New York

Whittinghill L, Rowe D. (2011). The role of green roof technology in urban agriculture. *Renewable Agriculture and Food Systems.* **27**(04):314–322

Wiener N. (1948). *Cybernetics, or, Control and Communication in the Animal and the Machine.* MIT Press, Cambridge

Williams J. (2019). Circular Cities: Challenges to implementing looping actions. *Sustainability.* **11**(2):423

Wu N, Silva E. (2011). Urban DNA: Exploring the Biological Metaphor of Urban Evolution with DG-ABC Model. *AGILE.* 1-7

Yamu C, Frankhauser P, (2015). Spatial accessibility to amenities, natural areas and urban green spaces: using a multiscale, multifractal simulation model for managing urban sprawl. *Environment and Planning B.* **42**:1054-1078

Zhabotinsky A. (1964). Periodical oxidation of malonic acid in solution (a study of the Belousov reaction kinetics). *Biofizika.* **9**:306-311

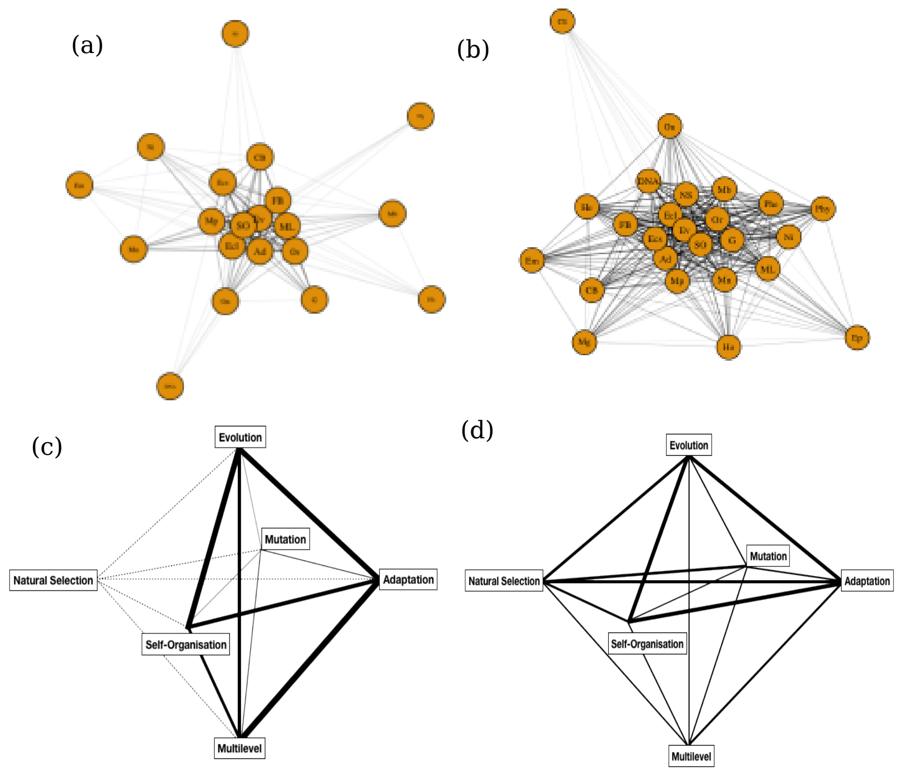



Figure 1. Word-map and key term linkage comparisons, showing the use of biological terms in studies examining self-organisation in (a) & (c) the urban design literature, (b) & (d) the biological literature. In (a) and (b) the letters refer to the terms: Ad=adaptation, CB=collective behaviour, CE=cultural evolution, DNA=DNA, Ecl=ecology, Ecs=ecosystem, Em=embryo, Ep=epigenetic, Ev=evolution, FB=feedback, G=gene, He=heritable, Ho=homology, Mb=metabolism, Mg=morphogenesis, Mp=morphology, ML=multilevel, Mu=mutation, NS=natural selection, Ni=niche, On=ontology, Or=organism, Pt=phenotype, Phy=phylogeny, SO=self-organisation. The size of the letters indicates the frequency of use and the darkness of the connecting lines indicates the frequency of the terms being used in the same papers. In (c) and (d) the width of the line represents the proportion of times terms are mentioned in the same paper. Dashed lines signify that the terms did not appear in the same paper. Terms not mentioned in any of the papers are not shown on the word maps.

(a)
(b)

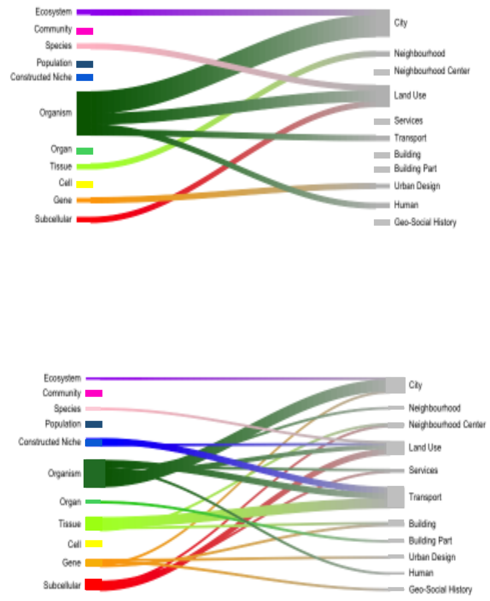



Figure 2.Mapping of the propensity for biological levels to be used as (a) analogies, and (b) analogies, metaphors and similes, for phenomena operating at urban levels. The thickness of the lines indicates the number of times the comparison was made.

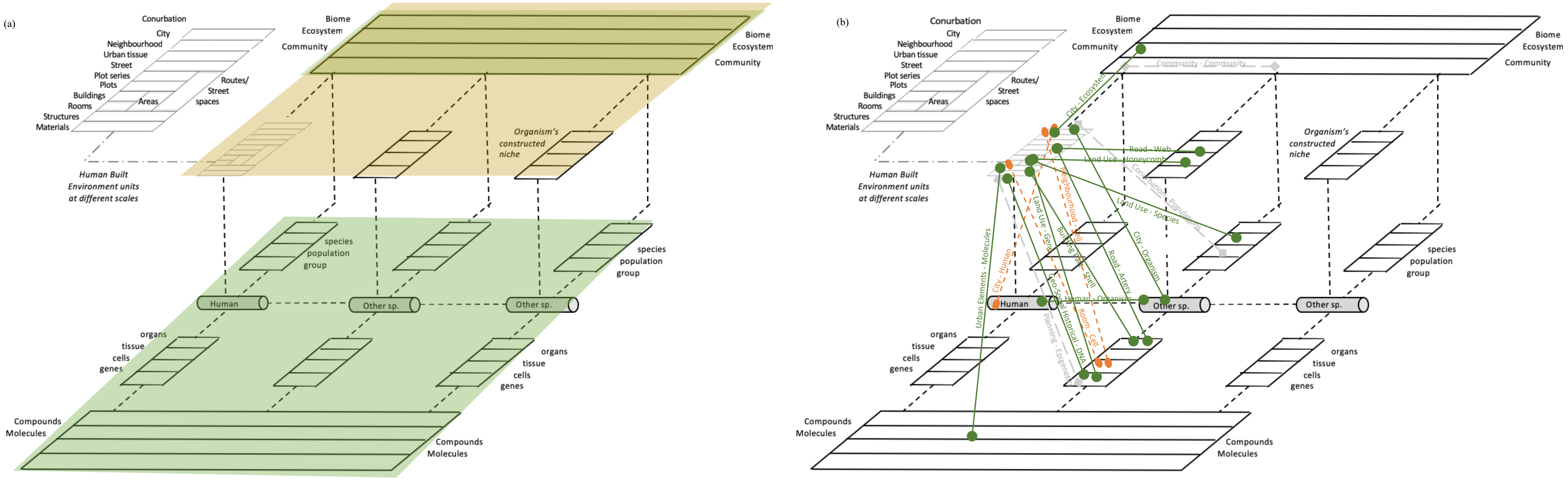



Figure 3. The Biotic Framework. (a) The left most section denotes the human realm, whilst the central and right most sections denote the natural world, focused on other organisms. The central nodes are the organism with lower hierarchical levels in the foreground and hierarchical levels containing the organism in the background. In the plane above that of the organism is its constructed niche and runs parallel to increasing organism number, signifying that, to varying extents, niche constructions affect all members of a species. The green represents organisms, their constituent parts etc., but excluding their constructions; the brown area represents the organisms' constructions and the brown/green zone represents where the part of the hierarchical levels where both organism and construction define the levels. (b) Analogical space where solid green coloured lines represent some of the biological comparisons identified during the literature review. Dashed orange lines represent 'classic' comparisons that we previously identified but did not fall within our literature sample (Sharpe and Wallock, 1987; Alexander, 1977; Bennett et al., 2003). Grey dashed lines represent potential analogies that we have identified using the biotic framework.

The (human) built environment structure (top left inset) is derived from (Kropf, 2014) and to which we have added 'neighbourhood', 'city' and 'conurbation'.

## Methods

*Identification of Journal Articles*

To investigate the use of biological inspiration in the urban self-organisation literature we identified five urban design related journals (Built Environment, Environment and Planning B: Planning and Design, Journal of Urban Design, Urban Design and Planning, Urban Design International) and five biology journals (Biology Letters, BMC Cell, Ecological Modelling, Ecology Letters, Theory in Biosciences), and extracted all articles mentioning self-organisation between 2000-2016 (Urban Design and Planning started in 2008 so its literature search spanned 2008-2016).



Articles were searched for using the advanced search tools in Google Scholar and Web of Knowledge. To account for differences in the spelling of self-organisation we searched for "self-organisation", "self-organization" for each of the 5 journals, limiting the results to since 2000. In Web of Knowledge we used "self-org*", the asterisk allows any combination of letters to follow the initial string. Once duplicates were removed 92 urban planning articles and 388 biological articles were downloaded.

For an article to be included in the study it had to mention self-organisation at least once in the body of the text, be a research or review article, thus eliminating articles such as editors' summaries of special issues and book reviews, and have been published between 2000 and 2016, articles published online in 2016 were included. In total 69 urban planning articles and 205 biological articles were found to meet the criteria and were examined further.

*Data Collection*

25 biological terms were selected because they either embodied fundamental or emerging concepts in biology e.g. evolution and epigenetics, were known to have been used previously by urban researchers e.g. metabolism, were relevant to self-organisation e.g. collective behaviour, or particularly relevant to the study of humans e.g. cultural evolution (a complete list is given in Figure 1). The frequency of each of these terms was recorded for each biological and urban paper. For a term to be counted it had to appear in the abstract or body of the article. Terms appearing in the title and sub-headings, figure captions, reference section, appendices etc were not counted.

All urban papers were read to identify how biological terms were used. The basic list of 25 terms was extended as the papers were read to ensure that biological comparisons that did not use one of our 25 terms were captured. Biological terms were classified by the mode of use: analogy, metaphor, simile, other. We employed definitions from the Oxford Dictionary of English (2017) to interpret these terms. As such, simile is defined as:

'*a figure of speech involving the comparison of one thing with another thing of a different kind, used to make a description more emphatic or vivid*',

metaphor as:

'*a figure of speech in which a word or phrase is applied to an object or action to which it is not literally applicable*',

and analogy as:

‘*a comparison between one thing and another, typically for the purpose of explanation or clarification’.*

However, there is much overlap between the use of these terms. Indeed, a simile is actually a type of metaphor, and analogies are often comprised of similes and metaphors, and so, we further distinguished simile as containing the words ‘*like*’ or ‘*as*’, and analogy as being a logical argument of similarity. As such, in our analysis, ‘*city is an organism*’ would always be noted as an analogy because (i) by itself it doesn’t make the description of the city more vivid or emphatic, rather it requires further metaphors or similes to clarify it, (ii) the phrase has a strong history of inspiring analogical thought, and as such, even alone, the reader may infer comparison of similarity. ‘*Arterial road*’, however, would not automatically be considered an analogy because no deeper meaning than main transport route is implied. ‘Arterial’ is a more vivid and emphatic synonym for main route than the word main.

For each urban paper the topic of the paper, whether or not an analogy was present and if it related to self-organisation was recorded. If a biological analogy was present the urban and biological agents that the analogy predominantly related were recorded (e.g. city - organism). Biological analogies were assessed on their clarity, biological soundness, depth and application using a scale of 1-5 (1=low, 5=high). Clarity referred to the unambiguousness of the analogy being made. Biological soundness to the accuracy of the biological information. Depth measured the amount of biological information included in the analogy, whilst application assessed the fit of the biological analogy to the urban realm.

*Statistical Analyses*

All statistical analyses and data visualisations were produced in RStudio using R version 3.4.0. In total, there were seven biological terms (including self-organisation) that appeared in one third or more of the urban planning papers (23 or more papers). The seven terms were 'adaptation', 'ecology', 'evolution', 'feedback', 'morphology', 'multi-level', and 'self-organisation'. The distribution of each term's usage was mapped using boxplots. As the data were non-parametric, two-tailed Wilcoxon-Mann-Whitney tests were used to examine differences in the likelihood that a particular term was used, between the two disciplines.

Mapping analyses were employed to compare differences and similarities in the handling of the 25 biological terms between the disciplines. Because the terms: 'cultural evolution', 'epigenetics', 'heredity', 'phenotype', and 'phylogeny' did not appear in the urban literature they were omitted from the mapping analysis. The Fructerman-Reingold layout was employed to distribute terms across the page, sending the least connected nodes furthest, whilst darkness of the lines between nodes was used to indicate the frequency with which the terms are used in the same paper.

The R library 'riverplot' was used to produce Sankey diagrams that graphically represent the frequency with which particular biological comparisons were employed in the urban literature.

To visualise the relationship between the clarity, depth, biological soundness and application of analogies, 3D scatterplots were employed as per Ligges et al. (2003). The points are anchored to a grid on the xy-axis to make clear their location. A linear model was calculated and plotted, resulting in a regression plane, from which the +ve (red lines) and -ve (blue dotted lines) residuals are drawn. The fourth dimension is shown using different symbol types.

**Results**

The number of urban articles mentioning self-organisation remained relatively constant between 2000-2011, rising between 2011-2016, a trend consistent with the findings of (de Bruijn and Gerrits, 2018; SM2). The number of biological papers mentioning self-organisation decreased after 2011, resulting in more urban papers being identified that contained self-organisation in 2016 than biological papers (SM2).

Self-organisation was referenced across a wide range of urban design topics (SM3). Discussion of self-organisation took many forms from models elucidating the mechanisms of urban self-organisation (Daffertshofer, 2001), the use of techniques to look for indicators of self-organisation (Chen and Zhou, 2006; Porta et al., 2006), unplanned, local initiatives such as guerilla gardening groups (Ache and Ferowitz, 2012; Silva, 2016), techniques for incorporating self-organisation into the planning process (Rauws and de Roo, 2016), to a cursory mention of self-organisation at some point in the article, for example as a potential area of interest for future research (Janssen-Jansen, 2013), or an intrinsic aspect of urban complex systems (Vancheri et al., 2008).

Kant and self-organisation's biological foundations were rarely mentioned; instead discussion of the history of self-organisation focused on the 20$^{th}$ century (Partanen, 2015) when major developments in the modern study of self-organisation occurred in the physical sciences.

*Biological Terms*

All urban papers contained at least one of our biological terms other than self-organisation. Self-organisation was the only term to appear in all 69 articles; however it was not the most used, appearing 474 times compared to the most popular biological term, evolution, found 497 times in 55 of the articles.

The frequency of use of 'self-organisation' was found to be consistent between the biological and urban literature (W=6355.5, $p$=0.1944). The same was true for adaptation (W=6656, $p$=0.4371) and feedback (W=7072.5, $p$=1). 'Ecology' was found to be employed significantly less in the urban literature (W=10852, $p$<0.001), whilst, 'evolution', 'morphology' and 'multi-level' were significantly more common in the urban than biological literature (W=5733, $p$<0.05; W=5595, $p$<0.001; W=5318.5, $p$<0.001, respectively, SM4).

Mapping of the terms revealed further inconsistencies in connections between the two disciplines (Fig.1). Whilst all 25 of our biological terms appeared in the biological literature, 'cultural evolution', 'epigenetics', 'heredity', 'phenotype', and 'phylogeny' did not appear in the urban literature. Of these, in the biological word map, 'heredity', 'phenotype', and 'phylogeny' are found on the outside edge of the central cluster, whilst 'cultural evolution' and 'epigenetics' were more distantly connected (Fig.1).

In both disciplines the strongest link is between 'self-organisation' and 'evolution', and both are linked to 'adaptation' (Fig.1). In the urban papers 'self-organisation' is also tightly bound to 'ecology', to which it is slightly less closely connected in the biological literature. From here, the two disciplines differ notably. Whilst, the biological mapping stresses the importance of 'gene', 'mutation', 'natural selection', 'organism', and 'morphology', the urban mapping highlights 'morphology', 'feedback', 'multilevel', and 'organism' (Fig.1).

This disparity and the discrepancy in central mapping of terms emphasises a key difference between the biological and urban realms. In biology, evolution is often defined in terms of changing allele frequencies in a population over time. New alleles enter a population in several ways e.g. mutation and immigration, whilst change is driven by gene flow, genetic drift and natural selection. Natural selection is the only mechanism that actively promotes organisms better adapted to their environment. Natural selection requires variation in the phenotypic expression of traits, that the expression of these traits is heritable between generations, and that these traits result in improved reproductive success. If so, individuals with beneficial traits reproduce more than individuals without beneficial traits, passing on those traits to their offspring, increasing trait occurrence in the population and so, the allele frequencies that underpin it. As such, the terms at the centre of the biological mapping all relate to biology's central theorem, that adaptive traits are the product of evolution through natural selection.

Direct analogues of biological evolution have been largely absent in urban planning (Mehmood, 2010). Those that do so face a multitude of challenges including: defining urban genes, characterising urban genes to phenotype translation, identifying the units of survival and reproduction, and defining urban fitness.

*Biological Comparisons*

In depth review of the urban articles resulted in the identification of 66 biological terms, which were used 2371 times. Biological comparisons were found in 31.88% of the urban articles. 15.94% of urban papers analogised the urban realm to the biological realm, 23.18% used metaphor, 7.25% similes (SM3). The total is more than 31.88% because some papers contained more than one type of biological comparison.

However, biological terms were more commonly used in a way *not* consciously invoking a biological comparison, e.g. "Cities are physical objects that display extreme variety of size and morphology" (Benguigui et al., 2001). Indeed, of the 2371 biological terms identified only 5.44%, 6.28%, and 2.91% were used as analogy, metaphor, or simile, respectively.

Of the 13 analogies identified, in 11 papers, 69.23% were made between entities at different hierarchical levels e.g. city–organism is cross-level analogy whilst person–organism is a direct level analogy (Fig.2). 38.46% of the analogies related directly to self-organisation. Where analogies were identified they were often found to be either unclear (mean=2, s.d.=1), and/or, of limited depth (mean=2.15, s.d.=1.07).; whilst, depth of analogy showed no connection with urban applicability of the analogy to the urban situation we found a positive association between the depth, and to a lesser extent the clarity, of an analogy and its biological soundness (SM5). The applicability of the biological analogue to the urban realm was found to be higher when it was both clearly conveyed and the biological content was accurate (SM5).

## References

Ache P, Ferowitz M. (2012). The Development of Co-Housing Initiatives in Germany. *Built Environment.* **37**(3):1–18

Benguigui L, Czamanski D, Marinov M. (2001). The Dynamics of Urban Morphology: The Case of Petah Tikvah. *Environment and Planning B.* **28**(3):447–460

Chen Y, Zhou Y. (2006). Reinterpreting Central Place Networks Using Ideas from Fractals and Self-Organized Criticality. *Environment and Planning B.* **33**(3):345–364

Daffertshofer A. (2001). Self-organized settlements. *Environment and Planning B.* **28**:89–102

de Bruijn E, Gerrits L. (2018). Epistemic Communities in Urban Self-organization: A Systematic Review and Assessment. *Journal of Planning Literature.* **33**(3):310–328

Janssen-Jansen L. (2013). Delivering Urban Intensification Outcomes in a Context of Discontinuous Growth: Experiences from the Netherlands. *Built Environment.* **39**(4):422–437

Ligges U, Mächler M. (2003). Scatterplot3d – an R Package for Visualizing Multivariate Data. *Journal of Statistical Software*. 8(11):1–20.

Mehmood A, (2010). On the History and Potentials of Evolutionary Metaphors in Urban Planning. *Planning Theory.* **9**(1):63–87

Oxford Dictionary of English (2017). Oxford University Press, Oxford. Dictionary app. Version 2.3.0 (203.16.12).

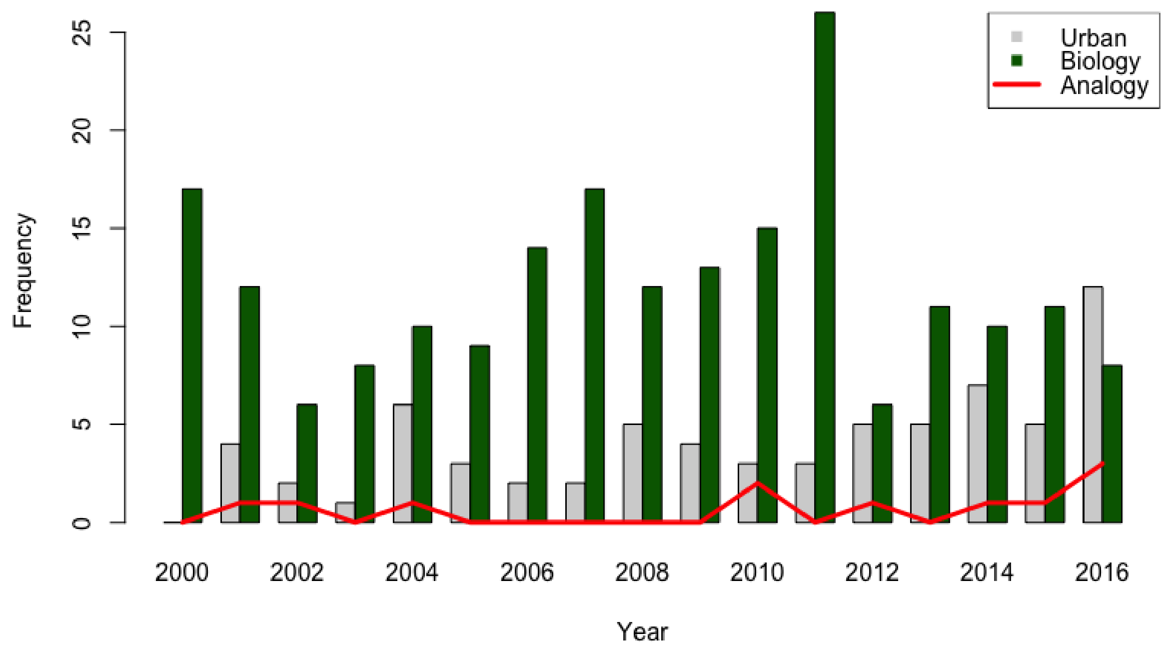
Partanen J. (2015). Indicators for self-organization potential in urban context. *Environment and Planning B.* **42**:951-971

Porta S, Crucitti P, Latora V. (2006). The Network Analysis of Urban Streets: A Primal Approach. *Environment and Planning B.* **33**(5):705–725

Rauws W, de Roo G. (2016). Adaptive planning: Generating conditions for urban adaptability. Lessons from Dutch organic development strategies. *Environment and Planning B.* **43**(6):1052–1074

Silva P. (2016). Tactical urbanism: Towards an evolutionary cities approach? *Environment and Planning B.* **43**(6):1040–1051

Vancheri A, Giordano P, Andrey D, Albeverio S. (2008). Urban growth processes joining cellular automata and multiagent systems. Part 1: theory and models. *Environment and Planning B.* **35**(4):723–739




Supplementary Material 2. Frequency plot of the number of articles using the term self-organisation found in the biological (green) and urban (grey) literature, and the frequency of urban articles containing a biological analogy, by year.

| Topic | No. S-O Papers | No. Papers with Analogy | Analogy |
|---|---|---|---|
| Urban Design/Planning | 12 | 4 | City is an organism or tree (Ganis et al., 2016)*.<br>City is an organism and tactical urbanism the energy for its evolution (Silva, 2016).<br>Metabolism is urban economy with city as organism (Girard, 2014).<br>Metabolism is urban economy with city as ecosystem (Girard, 2014).<br>Assembly of molecules to form life akin to assembly of elements to form cities, including translational mechanisms e.g. genetic blueprints (Salingaros, 2010).<br>City as living organism where rules govern structural and functional complexity and the breakdown of these rules leads to pathologies (Salingaros, 2010). |
| Methods | 20 | 2 | Parts of the city are species in an ecosystem (Partanen, 2015).<br>City is a multistructural organism (Frenkel, 2004). |
| Transport | 7 | 2 | Slime mould formation of transport networks (Adamatzky et al., 2017)**.<br>Collective behaviour of people like that of bird swarms (Helbing et al., 2001). |
| Urban Growth | 4 | 2 | Slime mould growth and urban growth (Barker, 2012).<br>Fitness of land uses is relative to the fitness of other land uses on the fitness landscape, least fit land uses are removed, most fit are added (Andersson et al., 2002). |
| Urban Morphology | 8 | 1 | Systems of internal body flow akin to human movement (Mehaffy et al., 2010). |
| Land Use | 9 | 0 | |
| Demographics | 3 | 0 | |
| Architecture | 1 | 0 | |
| Environmental | 1 | 0 | |
| Governance | 1 | 0 | |
| Housing | 1 | 0 | |
| Philosophy | 1 | 0 | |
| Policy | 1 | 0 | |

Supplementary Material 3. Articles included in the literature review by topic of article. Analogies are described where present. The table is sorted by (i) number of papers with analogies, (ii) number of self-organisation papers. * signifies where the analogy was used during a critique of analogy and was not presented as the authors' own. ** signifies that the article was published online in 2016.

## References

Adamatzky A, Allard O, Jones J, Armstrong R. (2017). Evaluation of French motorway network in relation to slime mould transport networks. *Environment and Planning B.* **44**(2):364–383

Andersson C, Rasmussen S, White R (2002) Urban Settlement Transitions. *Environment and Planning B.* **29**(6):841–865

Barker D. (2012). Slime Mold Cities. *Environment and Planning B.* **39**(2):262–286

Frenkel A. (2004). Land-use patterns in the classification of cities: the Israeli case. *Environment and Planning B.* **31**:711–730

Ganis M, Minnery J, Mateo-Babiano I. (2016). Planning people-places: A small world network paradigm for masterplanning with people in mind. *Environment and Planning B.* **43**(6):1075–1095

Girard L. (2014). Creative Initiatives in Small Cities Management: The Landscape as an Engine for Local Development. *Built Environment.* **40**(4):475–496

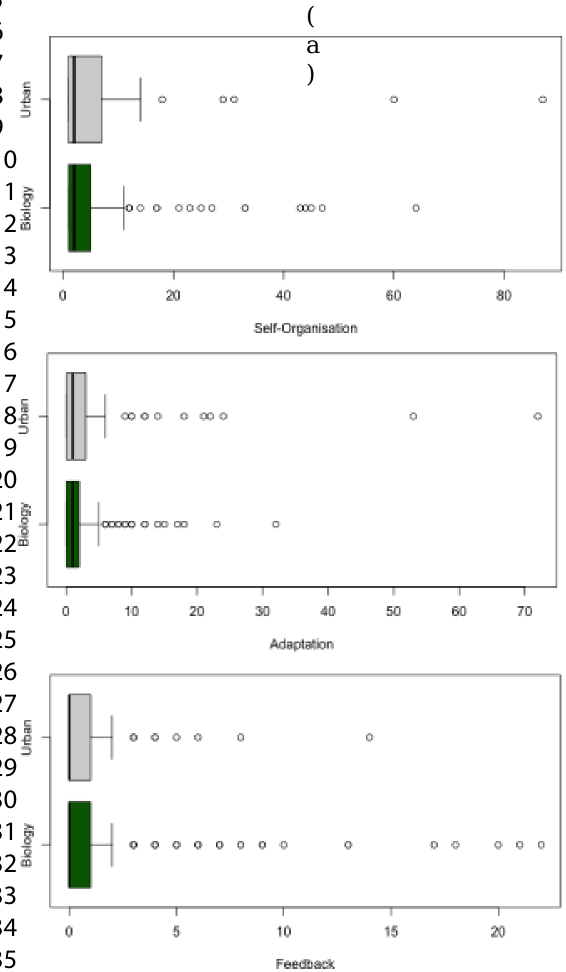
Helbing D, Farkas I, Molnar P, Bolay K. (2001). Self-organizing pedestrian movement. *Environment and Planning B.* **28**:361–383

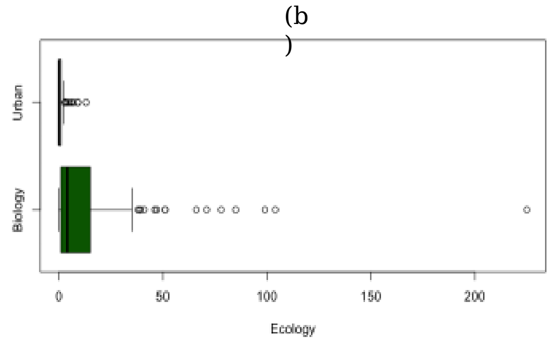
Mehaffy M, Porta S, Rofè Y, Salingaros N. (2010). Urban nuclei and the geometry of streets: The 'emergent neighborhoods' model. *URBAN DESIGN International.* **15**(1):22–46

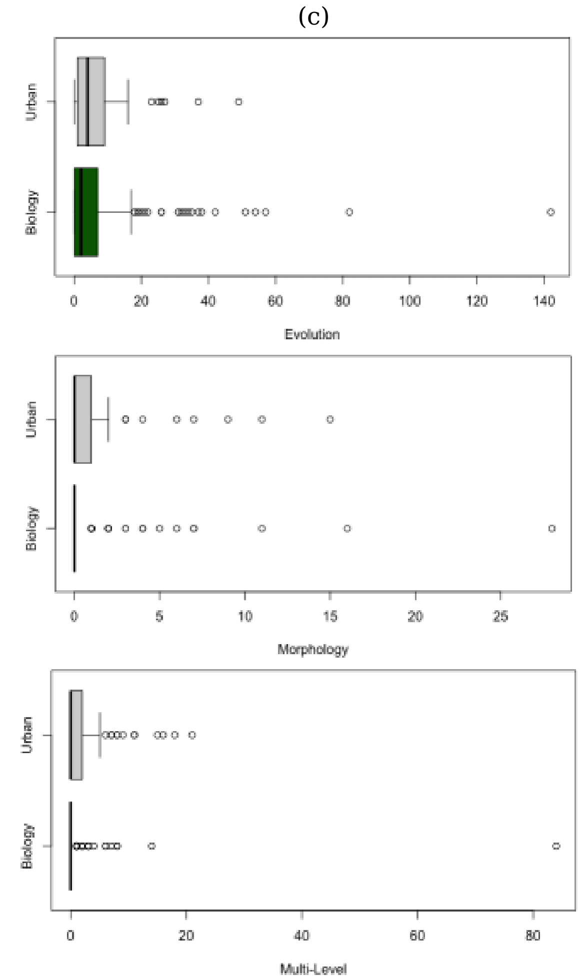
Partanen J. (2015) Indicators for self-organization potential in urban context. *Environment and Planning B.* **42**:951–971

Salingaros N. (2010). Complexity and Urban Coherence. *Journal of Urban Design.* **5**(3):291–316

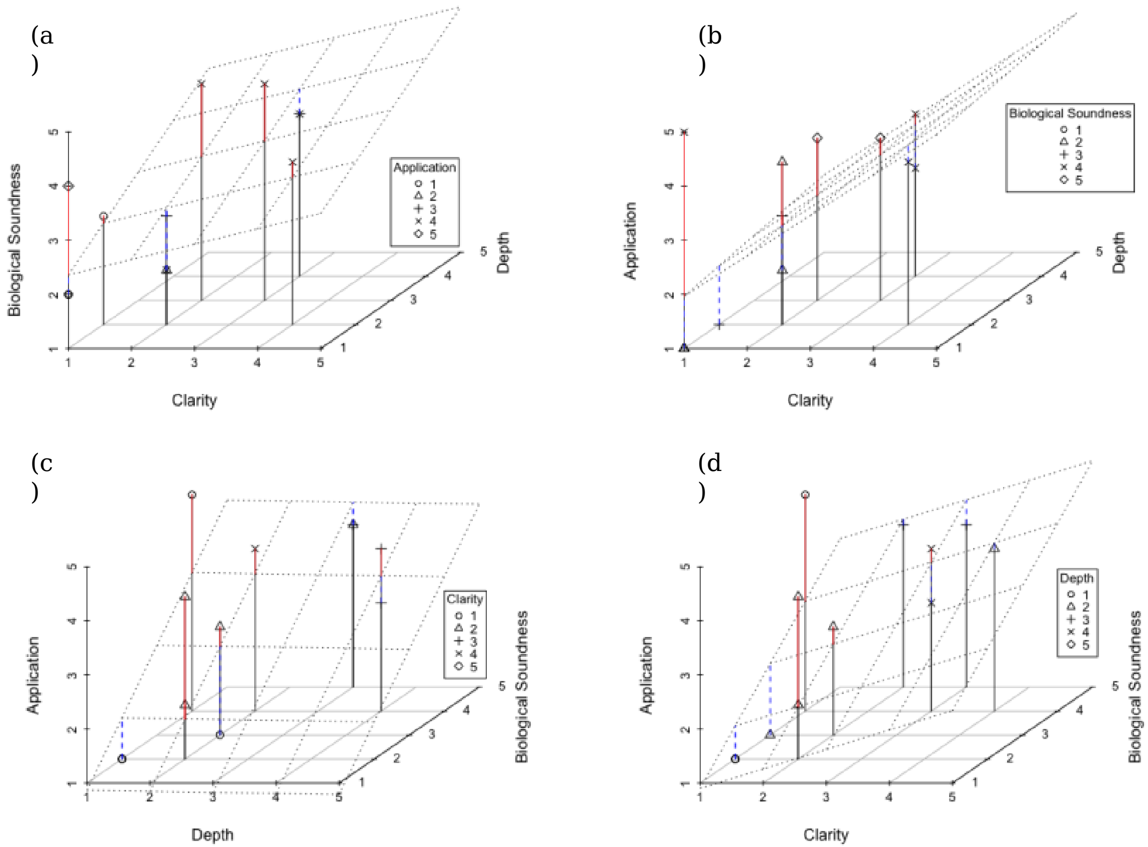
Silva P. (2016). Tactical urbanism: Towards an evolutionary cities approach? *Environment and Planning B.* **43**(6):1040–1051




Supplementary Material 4. Frequency distribution of the use of 5 biological terms in the urban (grey) and biological (green) literature. The dark line inside boxes represents the median. The terms in column (a) – self-organisation, adaptation, and feedback – were used similarly between the biological and urban literature. In column (b) – Ecology – the term was used significantly more in the biological literature. Terms in column (c) – Evolution, Morphology, and Multi-level – were significantly more common in the urban than biological literature.




Supplementary Material 5. Scatterplots showing the relationship between the clarity, depth, biological soundness and application of analogies in the urban planning literature. The point symbols show the fourth dimension. The black lines indicate the points position on the xy-axis. The red lines are the positive residuals, and blue-dashed lines the negative residuals, from the regression plane, drawn using a linear model.

## Introduction

Nature has inspired urban designers since they first attempted to understand the complex functional order of cities. Cities have been seen as organisms (Mumford, 1938; 1961) or ecosystems (Girard, 2014; Marshall, 2009); comprising components analogous with cells, tissues, organs, flesh, blood, tentacles and skeletons (Le Corbusier, 1947; Mumford, 1938; Soria y Mata, 1998); and subject to urban growth, morphogenesis, metabolism, adaptation and evolution (Geddes, 1915; Marshall, 2009; Rogers, 1998). Mining of other disciplines for inspiration and describing phenomena using analogies, metaphors and similes has advanced understanding of urban problems and investigation of possible solutions, as seen in the proliferation of biomimicry solutions for designing more sustainable cities (Benyus, 2009), evacuation routes (Dias et al., 2013), and new building materials (Vogel, 1998).

However, amid the profusion of biological comparisons it remains unclear whether or not usage is consistent or biologically robust. In these circumstances, biological analogies risk being dismissed as unscientific, or merely figures of speech, so opportunities for their advancement of understanding and application may be missed. As ‘nature-based solutions’ and scientific approaches to urbanism (Batty, 2012; Marshall, 2012) gain increasing attention, drawing inspiration from appropriate models (Batty, 2007; Moroni, 2015), analogies (Steadman, 2008), and metaphors (Chettiparamb, 2006; Tippett, 2010), it is an opportune time to revisit the nature of biological analogies in a systematic way.

Overall this mission would imply an extensive research agenda, potentially tracking relationships between biological and urban phenomena on multiple fronts, including processes such as self-organisation, metabolism, adaptation and evolution. As a first step, this paper addresses self-organisation.

Self-organisation refers to a bottom-up process where pattern emerges from numerous interactions among the components of an initially unpatterned system. Self-organisation does not require sentience of the self-organising units or an external agent. Rather, pattern emerges through local interactions between the system's components using positive and negative feedback.

Self-organisation research occurs across the natural and physical sciences, and urban researchers have drawn upon these to inspire bottom-up approaches to generating urban order (Batty, 1998; Portugali, 1997). It is an inherently cross-disciplinary domain, routinely recognised as having both biological and non-biological manifestations, with direct operational equivalences that go beyond the figurative. Consequently, our treatment of self-organisation provides a lens through which to study phenomena spanning the biological and the urban, offering a model for future application to other areas where biology has influenced urban design including development, adaptation, and evolution.

Here, our aims are to (i) identify a set of analogies, metaphors and similes based on self-organisation that are used in urban design; (ii) for analogies, establish a method for assessing their clarity, depth, and application to urban design; (iii) assess the validity of analogies according to contemporary biology; (iv) explore how these analogies link up or relate to each other in a more systematic way; and hence (v) establish a framework which contains and expresses the observed urban/biological relationships, and may also be used to generate new ones. We believe that this is a potentially pioneering agenda, generating a method that could find further application in other contexts, and wherein the scrutiny from contemporary biology is itself novel, yielding insights that are correspondingly original.

First, we briefly introduce the history of self-organisation and its current use in urban design and biology. Secondly, we undertake a systematic analysis of analogy between urban and biological disciplines, quantifying the use of analogy, and their biological validity. Finally, we suggest a new biotic framework through which to interpret the analogical space, locating existing analogies in relation to each other and helping to stimulate new analogies for urban application.

**Self-Organisation**

Whilst the idea that order can emerge by itself dates back to Democritus and Lucretius, it was Emmanual Kant who first coined the term 'self-organisation' arguing that organised beings can be distinguished from non-living entities because they have a self-organising 'formative power' which propagates itself that required a new type of science to explain it, because neither physics nor chemistry could (Karsenti, 2008; Keller, 2008).

Kant's 'new science' emerged much later, after his ideas received a series of rejections and revocations (Keller, 2008). A major challenge was that biology is largely based on chemical and biochemical reactions which don't self-organise (Tabony, 2006). Lotka (1909; 1925) submitted that chemical reactions might self-organise into oscillating chemical systems, akin to predator-prey population size dynamics, later confirmed experimentally by Belousov (1951) and Zhabotinsky (1964) and mathematically by Turing (1952). Interest proliferated across fields, leading to new understanding of the thermodynamic properties of dissipative systems (Prigogine and Nicolis, 1967), cybernetics and feedback (Ashby, 1960; Wiener, 1948), synergetics (Haken, 1977), fractals (Mandelbrot, 1982) etc. Such studies ushered in a new era in self-organisation research where both the animate and inanimate were products of self-organisation in nonlinear, far-from-equilibrium, open systems, and their results have been applied across the social, computational, economic, physical and biological sciences (Keller, 2009).

In biology, Goldbeter and Lefever (1972) used Belousov-like equations to describe glycolytic oscillations, and Turing's work has been applied to pattern formation in mammals' coats (Murray, 1988), and embryogenesis (Glover et al., 2017). Today, self-organisation research spans all levels of biological complexity, from micro: formation of the first polymers (Freire, 2015) and cell division (Karsenti, 2008); to macro: schooling fish (Camazine et al., 2001), species distributions (Alados et al., 2007), ecosystems (Lenton et al., 2018).

Urbanists also adopted self-organisation from the physical sciences. Prigogine's theory of dissipative systems was applied to the appearance of central places (Allen et al., 1985). Portugali (Haken and Portugali, 1996; Portugali, 1997) introduced synergetics, Batty and Xie (1997) pioneered cellular automata techniques, and both men applied fractal and synergetic approaches to chaos theory (Batty and Longley, 1994; Portugali, 1997). Today, self-organisation is routinely considered a central process in urban development (Yamu and Frankhauser, 2015) yielding important insights for urban planners considering topics including: urban intensification (Janssen-Jansen, 2013), urban codes (Moroni, 2015) and self-governance (Rauws and de Roo, 2016); for a recent mapping of research see de Bruijn and Gerrits (2018).

As biology has drawn from the physical sciences, urban designers are applying biological self-organisation to urban environments. Indeed, the richest potential for understanding urban self-organisation would appear to lie in learning from biology, which exhibits the fullest range of self-organising phenomena, from inanimate biomolecules through the animate world of sentient beings to ecosystems and Gaia. As such, a key challenge is to clarify how the biological component of self-organisation is being related to urban processes and where further insights might be found.

## Methods

To ~~address this challenge~~examine how biological inspiration is being used within studies of urban self-organisation we identified all articles referencing self-organisation between 2000-2016 in five urban design and five biology journals, resulting in 69 urban design and 205 biological articles. We listed 25 biological terms (Fig.1) and recorded their frequency per paper. Biology-inspired similes, metaphors and analogies were identified in the urban literature, and analogies were assessed for clarity, depth, biological soundness, and applicability using a 1 to 5 scale (1=low, 5=high). We used mapping analyses and boxplots to compare term usage between disciplines, and Sankey diagrams and 3D-scatterplots to assess how analogies were employed. For a fuller version of the methods and results see SM1.



## Results

The number of urban articles referring to self-organisation increased overall between 2000-2016 (SM2), and covered a wide range of urban design topics (SM3) including mechanistic models, unplanned-local initiatives, and the planning process.

### *Biological Terms*

All urban papers contained at least one of our biological terms other than self-organisation.

Mapping of terms revealed inconsistencies in connections between the two disciplines (Fig.1) highlighting differences in the way the terms are used (SM4).

[Fig.1]

In both disciplines the closest links were between ‘self-organisation’ and ‘evolution’. ‘Adaptation’ and ‘ecology’ are also closely connected, after which, the two disciplines diverge. The biological mapping stressing the importance of ‘gene’, ‘mutation’, ‘natural selection’, ‘organism’, and ‘morphology’, the urban mapping highlighting ‘morphology’, ‘feedback’, ‘multilevel’, and ‘organism’ (Fig.1).

Herein lies a key difference between the biological and urban realms. The biological mapping points to biology’s central theorem: that an <u>organism’s</u> <u>adaptive</u> traits are the product of <u>evolution</u> through <u>natural selection</u> and <u>mutation</u> is one mechanism of introducing genetic variation. Direct analogues of biological evolution are largely absent in urban planning (Mehmood, 2010), because those that do so face significant challenges including: defining urban genes and fitness, characterising urban gene to phenotype translation, identifying the units of survival and reproduction.

*Biological Comparisons*

Through further review of the urban articles 66 biological terms were identified, which were used 2371 times. Biological terms were most often used *without* consciously invoking a biological comparison; despite this, 31.88% of urban articles contained a biological comparison: 15.94% analogy, 23.18% metaphor, 7.25% similes (The sum is more than 31.88% as some papers contained more than one kind of biological comparison. SM3)

Thirteen analogies were identified, in eleven papers. 69.23% of which were made between different hierarchical levels e.g. city–organism is cross-level analogy, person–organism is a direct-level analogy (Fig.2). 38.46% of the analogies related directly to self-organisation. Analogies were often found to be either unclear (mean=2, s.d.=1), and/or, of limited depth (mean=2.15, s.d.=1.07); whilst depth of analogy showed no connection with urban applicability we found a positive association between the depth, and to a lesser extent the clarity, of an analogy and its biological soundness (SM5). Applicability was found to be higher when an analogue was both clearly conveyed and the biological content was accurate (SM5).

[Fig.2]

**Nature-Inspired Urbanism?**

*Depth, Clarity, Biological Soundness*

Overall, the analogies lacked depth and clarity. Lack of depth had nominal effect on the applicability of an analogy to the urban realm. Rather, the more reliable the biological basis, and the more clearly the information was applied, the better the fit of the biological analogue. As depth and clarity increased, the biological information was found to be more dependable, a not wholly surprising result as clarity and depth are both qualities required to adequately assess biological content.

That an analogy was not required to be deep to be successful is more interesting. An analogy may be so commonly employed that in-depth interrogation is not required to impart meaning e.g. city is organism. The purpose of the analogy may not call for an in-depth analysis of biological theory. Or, the biological connection may not be particularly important to the author, who instead could opt for deeper analogies with other disciplines, which may themselves be analogous, and produce similar insights (Helbing et al., 2001).

Concerningly a lack of depth and/or clarity can make it difficult to distinguish the type of biological comparison being used, leaving readers to infer meaning according to their own biases. For example, depending on the author, and reader, city as organism may be purely symbolic (Nientied, 2016), or an analogy from which logical arguments can be extended and planning decisions made (Golubiewski, 2012). Combine this with terms having multiple definitions or context sensitivity and it is easy to see how confusion may occur.

All of these are common problems facing writers who use comparative language to express ideas (Chettiparamb, 2006). However, with over half of the world's population inhabiting cities and increasing disconnection from the natural environment (Cox et al., 2017), urban authors face a more fundamental problem when using biological comparisons: that of using the unfamiliar to describe the familiar.

Urban DNA is a particularly interesting example (Boelens, 2014; Nientied, 2016; Wu and Silva, 2011). Whilst DNA is a part of us, it is not a part we see or feel, or identified the role of until Avery et al. (1944). Thanks to the efficacy of language, art, and the fundamental desire to understand the nature of being, DNA has become relatable. Its structure, the information it inscribes and 'mystical powers' have been described as a twisted ladder, a blueprint, an immortal spiral (Rovira, 2008).

The particular comparisons employed can markedly alter our understanding, and the implications, of a concept. Informational and essentialist DNA metaphors have shaped our laws (Silvestro, 2016), and metaphors regarding DNA's components have shaped research trajectories (Avise, 2001). New findings may invalidate descriptors, eliciting calls for their alteration or discontinuation e.g. 'DNA is a blueprint' lost favour because it implies a direct mapping of genetic information to phenotype, when in actuality, the same genetic code can produce remarkably different phenotypes e.g. queen and worker honeybees. Perhaps 'genetic code' remains in good standing because 'code' does not suggest decryption method, allowing many final forms and the capacity to integrate new research findings. As such, the analogy of urban DNA might better be conceptualised as a set of generative codes, or framework rules, resulting in a self-organised urban order, as opposed to urban order generated by a blueprint.

Ultimately, research requires the clear communication of ideas, so they can be assessed and discussed. Where confusion occurs advancement is hampered (Steadman, 2008). Defining terms and the limits of one's analogies can help reduce confusion, clarify thinking, and elucidate when a field where inspiration is being drawn from is itself using the same term in different ways. For example, in biology, terms such as metabolism are regularly used across disciplines and hierarchical levels but refer to different processes (Golubiewski, 2012). Thus, referring to the city as ecosystem and as organism, particularly in the same paper, can have very different implications, muddling the narrative.

*Description, Inspiration, and Mechanism*

Analogies were used to either describe, inspire or suggest mechanism. In description, the opportunity for an extended metaphor to be confused for analogy was highest. For example, is Frenkel's (2004) description of cities as '*multistructural organisms as reflected in the spectrum of their functions*' and use of taxonomic methods to '*classify cities according to their characteristics*' a metaphor, or an obvious extension to the commonly expressed analogy?

Inspirational analogies encouraged new ways of thinking about the urban environment. Salingaros (2010) used the earliest bio-molecules to inspire urbanists to look beyond an urban element's primary function to consider secondary and potential catalytic effects. Finally, mechanistic analogies such as Barker (2012) and Adamatzky et al. (2017) who employed different slime mould species to reveal how simple, local, bottom-up interactions lead to urban formation and efficient transport networks, respectively.

Three of the five analogies that proposed mechanism were directly related to self-organisation. Of course, as self-organisation is a mechanism this correlation is unsurprising. More interesting is that two of these three studies drew comparisons of urban systems from the behaviour of slime moulds, which, over recent years, have helped overturn notions of the minimum level of intelligence needed to solve complex problems, leading to the development of simpler algorithms to solve modern day human problems.

Difficulties arise in that: models have mostly been deductive rather than predictive, limiting their current value to urban planning (Adamatzky et al., 2017); the focus on economic 'rationality' can favour highly productive regions rather than the growth of underdeveloped regions (Vanoutrive et al., 2016); the spatial scale and morphology of slime mould experiments may dramatically change the solutions arrived at and might not always be optimal (Reid et al., 2012), as slime moulds can make irrational decisions, similar to humans (Latty and Beekman, 2010).

Examining a variety of organisms may be more informative to urban planners, providing a variety of solutions to choose from. For example, Argentine ant (*Linepithema humile*) networks prioritise cost and efficiency over robustness (Cabanes et al., 2014), the fungus *Phanerochaete velutina*'s networks maximise robustness and efficiency (Bebber et al., 2007), whilst the networks of wild polydomous ant colonies, which can stretch thousands of kilometres, have more connections than those found in lab populations, suggesting robustness may be a more important factor in ecologically valid situations (Cook et al., 2014).

*Analogies Across Levels of Scale*

Both biological and urban systems are characterised by nested levels of increasing complexity, where each level is primarily composed of the level below but possesses emergent properties not present in that level. Mechanisms leading to the spatial organisation of lower level entities forming higher hierarchical levels include self-organisation, environmental constraint, and cooperation {MaynardSmith:1995wr, Takeuchi:2009el},

Biological levels extend from molecules to Gaia, although authors generally define a narrower, question-appropriate range. The delineation between biological hierarchies is not as neat as it might initially appear. Single celled organisms, for example, inhabit both the cell and organismal levels, and an organism is a community, called the holobiont, when microbiome, virome and parasites are accounted for.

The urban realm can include human concepts of geographical/economical/political areas but, for most urban researchers their questions will fall between the people and regions levels, and like biological levels of organisation, delineation between urban levels and elements at different scales is not always clear cut (Alexander et al., 1977; Kropf, 2014). Actually, the urban hierarchy is nested within the biological hierarchy. People are organisms so are found on the biological hierarchy at the level of organism. The urban environment is a type of ecosystem; however, it can also be considered at lower hierarchical levels (e.g. community), depending on the question being asked.

Most of the analogies we identified crossed hierarchical levels (Fig.2), analogising city to organism, land uses to genes, and pedestrian paths to capillaries. Analogies existing at equivalent hierarchical levels included city as ecosystem and models derived from slime moulds because, whilst a slime mould and transport network (for example) may not immediately appear to be at the same hierarchical level, the rules for their formation are both generated at the organismal level, for modern human transport networks are often founded atop the informal, emergent trails of our ancestors.

Logically, all analogies that operate below the level of the organism must be cross-level analogies. However, an interesting anomaly may occur with plan/blueprint/design as urban 'genotype'. A plan/design is neither nested within nor essential for the construction or functioning of higher-level entities. Indeed, it may merely be a representation of a completed form, rather than its generator. What is nested within and essential to the construction and functioning of urban form is the urban population, each with genomes, and so, one could postulate that *people* are the urban genotype.

Employing evolutionary analogy Silva (2016) states that tactical urbanism (a self-organised approach that transform the urban environment through self-built interventions) provides the 'energy' for urban evolution, implying 'energy' translates to mutation. However, tactical urbanism can be more clearly and instructively described in terms of niche construction where, rather than city as organism it is analogous to a hive, burrow etc.

Niche construction theory is a broadening of Dawkins' (1982) extended phenotype hypothesis such that any manipulation of the environment by the organisms inhabiting it, and the effects of those manipulations on adaptive fitness of the organism, its progeny and other organisms in the environment, are now included (Odling-Smee et al., 2003).

Niche construction theory recognises that by altering their environments organisms alter the selection pressures acting upon them, such that the organism adapts to the environment *and* the environment adapts to the organism. Thus, the organism produces an ecological inheritance (Odling-Smee et al., 2003) which, if fitness enhancing, will promote co-evolution of trait and constructed niche. In social groups, cultural inheritance can also drive niche construction (Ellis, 2015; Kendal et al., 2011).

Theoretical examinations integrating ecological and cultural inheritances have found that niche construction is capable of overriding, reversing or accelerating natural selection, and of generating unusual population dynamics (Laland and Brown, 2006; Laland et al., 2001). Further, gene-culture-co-evolution has been proposed as the dominant mechanism of adaptation in humans (Ellis, 2015; Laland et al., 2010). Therefore, the creation of the human built environment is not only part of urban evolution, it is a part of human evolution, past and present. In other words, '*we co-evolve with the environment we create*' (Kropf, 2017).

It is often self-organisation, operating amongst individuals or across environmental components, that shapes constructed niches. Social insects build nests, orders of magnitude larger than an individual through self-organised collective action, following cues derived internally, from nestmates, or environmentally (Green et al., 2017). Architecture has produced buildings inspired by social insect nests but none has captured the adaptive quality of nest architecture, where structure and function have become one, and mechanism is derived through a ~~homeostatic~~ desire to maintain a stable internal environment that can be cognitively and physiologically produced (Penn and Turner, 2018; Turner and Soar, 2010).

Returning to the example of tactical urbanism: as in niche construction theory, tactical urbanism denotes a self-organised, bottom-up approach, that transforms the urban environment, through self-built interventions (Silva, 2016), rather than being a mutation in an organism. Tactical urbanism initiatives include 'Guerrilla Gardening', 'Intersection Repair', 'Pop-up Cafes'. Their role seems often to beautify and connect, and these homeostatic desires could be routed in a physiologically evolved need to reduce stress. When possible, portions of the urban population may be intuitively transforming their environments, removing or reducing aspects that negatively impact fitness. In doing so, they not only enhance their own fitness but that of their neighbours, increasing the probability of accruing benefits through reciprocal altruism or kin selected benefits. The fitness enhancement may, today, be small, but for the urban planner, the lessons may be of use. Firstly, such initiatives are likely excellent venues of inspiration for positive design ideas that can be extended more widely. Thus, allowing space for citizen-led, self-organised, bottom-up approaches to exist is of great import. Secondly, urban planners could co-opt this mechanism by identifying ways to translate innate homeostatic preferences into urban design, enabling the urban population to alter their environments for public good by building environmental feedback mechanisms into architecture (Pasquero and Zaroukas, 2016).

**Analogical Space to Biotic Framework**

Our analysis revealed a preponderance of cross-level comparisons over equivalences (direct-level analogies). Indeed, even when a level of equivalence was being evoked it was often masked. Barker (2012), for instance, modelled how land-use decisions generate cities, where the model and decision rules were inspired by self-organised slime mould agglomerations~~slime mould agglomeration behaviour~~. That the land-use decisions are made by humans and the model is using slime mould behaviour to propose simple rules underpinning human behaviour, is not explicitly stated. Operating so, the urban literature risks overlooking key areas of instructive insights that fall at the level of equivalence.

In biology, evidence accrues through analogous research across taxa, where different evolutionary and life histories lead to different predictions drawn from the same theory. In feeding into these bodies of literature direct-level analogies (equivalences) could provide a more substantial contribution to urban researchers than the purely figurative. For, after all, humans are organisms too.

To demonstrate our thinking we propose the biotic framework (Fig.3) – so named because it emphasises that both organisms and their constructed environments are biotic - relating to or resulting from living organisms. In a very literal sense, our cities, indeed all human environmental modifications, are biotic. Our emphasis on the biotic is in contradistinction to traditional emphases on human versus nature, or organic versus inorganic – though both of these form part of the framework.

[Fig.3]

The framework provides a rationale for locating and identifying analogies, particularly those where the processes operating are most likely to be comparable to urban processes, and encourages awareness of the entire system. We present two versions of the biotic framework (a) presenting the framework and its dimensions, (b) showing a subset of the biological comparisons identified in the reviewed literature (green solid lines), some well-known comparisons that not present in the reviewed literature (orange dashed lines), and some connections that we suggest could provide new inspiration for urban designers (grey dashed lines) (Fig.3).

Protruding into the foreground are the lower hierarchical levels. At the front are biomolecules and compounds which form the basis of life, composing every living organism, prompting 'the continuity thesis' which suggests that there is no break between physiochemical and biological systems (Freire, 2015). The coalescence of molecules forms the constituent parts of cells, which come together to form tissues, organs, and organism.

Biological comparisons between urban elements and levels below that of organism have proved popular, inspiring new conceptions of urban environments and processes. Comparisons made between molecules (Salingaros, 2010), or parts of an organism (Furtado et al., 2012; Mehaffy et al., 2010; Salingaros, 2010), and the urban environment are, by definition, cross-level analogies. Whilst there is no denying the merits of such comparisons, we propose that, where an analogy relates to process, inspiration will more readily be found and likely better fit the example, when it is drawn at the level of equivalence.

The level of the organism is the first hierarchical level where drawing upon equivalence is possible. Here, the living entity, be it human, slime mould, ant, or bower bird, is the focus. Its cognition, behaviour, and decision making, are of primary importance because such rules determine how organisms use, move around and understand the environment, and population distributions. At this level, natural and cultural selection play dominant roles in shaping the behavioural rules and physiological requirements of the organism.

Moving into the diagram from the position of the organism, two planes run parallel, the lower signifying increasingly large clusterings of the same organism (group, population, species), the upper signifying the organism's constructed environment. We adopt the definition from niche construction theory to characterise a constructed environment - any modification of the environment by an organism which alters the selective pressures acting upon it and other organisms inhabiting that environment. As such, constructed niches vary dramatically between organisms including leaf litterfall (Bigelow and Canham, 2015), birdsong repertoire size (Creanza et al., 2015), and termite mega-structures (Turner, 2004). The two planes run parallel because to differing extents the constructed niche will impact the selective pressures acting on those groupings.

To represent hierarchical relationships between elements within the human built environment we build upon a representation proposed by (Kropf, 2014), adding neighbourhood, city and conurbation as familiar reference points, although these do not imply an exact structural continuation of the lower levels.

Humans, like all organisms, don't inhabit the world alone or immune from the effects of the environment. When organisms interact they form communities; the combination of communities and physical processes are ecosystems, which in turn combine to biomes and eventually Gaia. At these levels, natural selection plays a muted role. Rather, system evolution and adaptation may be guided by self-organised mechanisms (Lenton et al., 2018). The urban environment is an ecosystem and so, analogies drawn between mechanisms of natural ecosystem functioning, resilience, evolution, adaptation etc., with urban processes are examples of equivalences.

As each hierarchical level is an emergent property from coalescence of the level below, disturbance at one level can trigger changes upwards and downwards. The biotic framework draws attention to the interconnected and hierarchical nature of the whole system and can be used to interrogate the implications of transformations across hierarchical levels. Analogy does not have to include multiple hierarchical levels to be of use. However, by considering the implications of an analogy across multiple hierarchical levels, and defining the limits of the analogy, not only are the clarity and biological soundness likely to be improved (a key indicator of the fit of an analogy to the urban realm) but the potential to identify novel insights is markedly increased.

Indeed, the framework motivated us to propose, for demonstrative purposes, three new comparisons, that might serve to inspire urban design and the rules that formulate urban environments. Firstly, ~~Secondly,~~ we refer back to transport networks and our assertion that examining networks of polydomous ant colonies may be instructive for urban planners, particularly as field studies show that networks of nests, analogous to a conurbation or network of cities, favour different network characteristics than lab colonies (Cook et al., 2014). Secondly, as initiatives work to bring food production into our urban environments (Whittinghill and Rowe, 2011) using natural communities to inspire our understanding of the needs of urban communities will become ever more crucial. A classic example of farming in animal societies is that of fungus farming ants; this turns out to be a multi-species mutualism (Barke et al., 2010) highlighting the need to consider community dynamics even within complex constructed niches, and the role of the constructed niche in shaping those communities and dynamics.~~.~~ ~~Secondly, we refer back to transport networks and our assertion that examining networks of polydomous ant colonies may be instructive for urban planners, particularly as field studies show that networks of nests, analogous to a conurbation or network of cities, favour different network characteristics than lab colonies (Cook et al., 2014).~~ Thirdly, we propose that epigenetic mechanisms for pattern formation (non-genetic influences on gene expression that affect traits such as coat pattern, caste differentiation, and that allow organisms to rapidly respond to changing environments) could ~~be used for inspiring a new type of responsive planning~~inspire a new (or newly recognised) layer of 'epigenetic' directions within urban design/planning. Such an epigenetic layer would guide where and when different codes or framework rules are deployed, perhaps in conjunction with outline planning or strategic zoning ~~(combined with, or as an alternative to, urban plans, codes or framework rules), making our cities more adaptive and resilient to future challenges,~~ formalising Moroni's (2015) suggestion of 'rules for the production of rules for the activation of processes' and/or integration of 'location-specific development regulations, traditionally expressed in the land-use plan, with generic regulations' {Rauws:2016hl}. In other words, the urban equivalent of epigenetic mechanisms could be used to help guide self-organising urbanism in a third way that offers a balance between more purely bottom-up or top down processes.~~.~~

**Conclusion**

Our research has found a rich diversity of biological analogies associated with urban phenomena relating to self-organisation but these are currently applied with limited depth and relation to each other. Still, they could be applied more deeply and systematically, and we show how via the biotic framework, which has also stimulated new analogies. We believe this analysis, including assessing the biological soundness of analogies, is original in a way unprecedented since the time of Patrick Geddes, and can pave the way for further research agendas, including application to other analogical processes (e.g. urban adaptation, evolution) and other disciplinary domains.

In our analysis we found that analogies between biological and urban realms were drawn from molecule to ecosystem and human to city. They mostly crossed hierarchical levels and the potential for confusion from the complexity of these different relationships led us to generate the biotic framework (Fig.3). This framework was initially created to articulate the analogical space that has been the focus of this paper, but in doing so provides a structure for conceptualising and interpreting relationships between key domains of the biotic sphere.

Our analysis suggests that attention could be usefully directed to the more direct analogies or equivalences because: cities are actually ecosystems; our built environments are actually constructed niches; our built environments have a material effect on our ongoing evolution. Furthermore, these three statements are linked and can be made more visually explicit via the biotic perspective. In addressing equivalence, insights from reading across human and natural realms may be particularly pertinent because they access overarching theories, built on evidence from a wide array of organisms, to explain and describe the evolution and mechanistic underpinnings of the phenomena.

For the urban environment, comparisons operating at the level of the organism and providing feedback between organism and environment will be particularly pertinent. Niche construction theory has already been applied to human evolution (Laland and Brown, 2006; Laland et al., 2001; 2010) and combining biological theory e.g. optimal foraging or cultural niche construction, with insights from past trends, could help identify planning perspectives that are adaptive, resilient, ~~and~~ commensurate with our ~~homeostatic~~ inherent desires for physiological comfort, and advance theory.

At higher ecological levels, the environmental effect of humans is ever more tangible. Calls to circularise our systems (Williams, 2019), or mimic the services provided by natural ecosystems (Benyus, 2009) do not benefit from the view of city as organism; rather, the view of cities as ecosystems, and drawing inspiration from natural ecosystem functioning, failures and resilience, provides a stronger basis from which to construct solutions to the ultimate problems facing future urban environments. As such, choosing the right analogy is not purely a choice of literary expression but, as with the example of DNA, can make a material difference to our perception of a problem and as such appropriate solutions.

Interestingly, the biotic framework can be seen as a freshly explicit expression of Geddes's understanding of the equivalence of the human and natural realms, that has more often remained implicit (Geddes, 1915). His assertions regarding the interaction between human evolution and environment invoke modern niche construction theory, his concept that cooperation overrides conflict is supported by multilevel selection theory. As biology furthers its understanding of evolutionary processes, self-organisation is emerging as a principal force, shaping form through the self-organised behaviours of organisms, and ecosystems through self-organising mechanisms far removed from the reach of the genes. This could provide an area for future application linking urban self-organisation and evolution. Overall, analogies at the level of equivalence could become of increasing interest, even to those wary of organicist metaphors, not despite their biological roots but because through them comparison can go beyond the purely figurative.

**References**

Adamatzky A, Allard O, Jones J, Armstrong R. (2017). Evaluation of French motorway network in relation to slime mould transport networks. *Environment and Planning B.* **44**(2):364–383

Alados C, Aich A, Komac B, Pueyo Y, García-Gonzalez R. (2007). Self-organized spatial patterns of vegetation in alpine grasslands. *Ecological Modelling.* **201**(2):233–242

Alexander C, Ishikawa S, Silverstein M, Jacobson M, Fiksdahl-King I, Angel S. (1977). *A pattern language: Towns, buildings and construction.* Oxford University Press, New York

Allen P, Sanglier M, Engelen G, Boon F. (1985). Towards a new synthesis in the modeling of evolving complex systems. *Environment and Planning B.* **12**(1):65–84

Ashby W. (1960). *Design for a Brain: the origin of adaptive behaviour.* Wiley, New York

Avery O, MacLeod C, McCarty M. (1944). Studies on the chemical nature of the substance inducing transformation of pneumococcal types. *Journal of Experimental Medicine.* **79**(2):137–158

Avise J. (2001). Evolving Genomic Metaphors: A New Look at the Language of DNA. *Science.* **294**:86-88

Barke J, Seipke R, Grüschow S, Heavens D, Drou N, Bibb M, Goss R, Yu D, Hutchings M. (2010). A mixed community of actinomycetes produce multiple antibiotics for the fungus farming ant *Acromyrmex octospinosus*. *BMC Biology.* **8**:109

Barker D. (2012). Slime Mold Cities. *Environment and Planning B.* **39**(2):262–286

Batty M. (1998). Urban Evolution on the Desktop: Simulation with the Use of Extended Cellular Automata. *Environment and Planning A.* **30**(11):1943–1967

Batty M. (2007). *Cities and Complexity: understanding cities with cellular automata, agent-based models, and fractals.* MIT Press, Cambridge (MA).

Batty M. (2012). Building a science of cities. *Cities.* **29**:S9–S16

Batty M, Longley P. (1994). *Fractal Cities: a geometry of form and function*. Academic Press, New York.

Batty M, Xie Y. (1997). Possible urban automata. *Environment and Planning B.* **24**:175–192

Bebber D, Hynes J, Darrah P, Boddy L, Fricker M. (2007). Biological solutions to transport network design. *Proceedings of the Royal Society B.* **274**(1623):2307–2315

Belousov B. (1951). *A periodic chemical reaction and its mechanism. Oscillations and travelling waves in chemical systems.* Wiley, New York.

Bennett J, Cooper M, Hunter M, Jardine L. (2003). *London's Leonardo: the life and work of Robert Hooke*. Oxford University Press, Oxford

Benyus J. (2009). Biomimicry in action. https://www.ted.com/talks/janine_benyus_biomimicry_in_action

Bigelow S, Canham C. (2015). Litterfall as a niche construction process in a northern hardwood forest. *Ecosphere.* **6**(7):117–14

Boelens L. (2014). Delta Governance: The DNA of a Specific Kind of Urbanization. *Built Environment.* **40**(2):169–183

Cabanes G, van Wilgenburg E, Beekman M, Latty T. (2014). Ants build transportation networks that optimize cost and efficiency at the expense of robustness. *Behavioral Ecology.* **26**(1):223–231

Camazine S, Deneubourg J-L, Franks N, Sneyd J, Bonabeau E, Theraula G. (2001). *Self-organization in biological systems.* Princeton University Press, Princeton.

Cook Z, Franks D, Robinson E. (2014). Efficiency and robustness of ant colony transportation networks. *Behavioral Ecology and Sociobiology.* **68**(3):509–517

Cox D, Hudson H, Shanahan D, Fuller R, Gaston K. (2017). The rarity of direct experiences of nature in an urban population. *Landscape and Urban Planning.* **160**:79–84

Creanza N, Fogarty L, Feldman M. (2015). Cultural niche construction of repertoire size and learning strategies in songbirds. *Evolutionary Ecology.* **30**(2):285–305

Dawkins R. (1982). *The Extended Phenotype*. Oxford University Press, Oxford

de Bruijn E, Gerrits L. (2018). Epistemic Communities in Urban Self-organization: A Systematic Review and Assessment. *Journal of Planning Literature.* **33**(3):310–328

Dias C, Sarvi M, Shiwakoti N, Ejtemai O, Burd M. (2013). Investigating collective escape behaviours in complex situations. *Safety Science.* **60**:87–94

Ellis E. (2015). Ecology in an antropogenic biosphere. *Ecological Monographs* **85**(3):287–331

Freire M. (2015). Nontemplate-driven polymers: clues to a minimal form of organization closure at the early stages of living systems. *Theory in Biosciences.* **134**(1-2):1–18

Frenkel A. (2004). Land-use patterns in the classification of cities: the Israeli case. *Environment and Planning B.* **31**:711–730

Furtado B, Ettema D, Ruiz R, Hurkens J, van Delden H. (2012). A cellular automata intraurban model with prices and income-differentiated actors. *Environment and Planning B.* **39**(5):897–924

Ganis M, Minnery J, Mateo-Babiano I. (2016). Planning people-places: A small world network paradigm for masterplanning with people in mind. *Environment and Planning B.* **43**(6):1075–1095

Geddes P. (1915). *Cities In Evolution*. Williams & Norgate, London

Girard L. (2014). Creative Initiatives in Small Cities Management: The Landscape as an Engine for Local Development. *Built Environment.* **40**(4):475–496

Glover J, Wells K, Matthäus F, Painter K, Ho W, Riddell J, Johansson J, Ford M, Jahoda C, Klika V, Mort R, Headon D. (2017). Hierarchical patterning modes orchestrate hair follicle morphogenesis. **15**(7):e2002117–31

Goldbeter A, Lefever R. (1972). Dissipative structures for an allosteric model: application to glycolytic oscillations. *Biophysical Journal.* **12**(10):1302–1315

Golubiewski N. (2012). Is There a Metabolism of an Urban Ecosystem? An Ecological Critique. *AMBIO.* **41**(7):751–764

Green B, Bardunias P, Turner J, Nagpal R, Werfel J. (2017). Excavation and aggregation as organizing factors in de novo construction by mound-building termites. *Proceedings of the Royal Society B.* **284**(1856):20162730–14

Haken H. (1977). *Synergetics: an introduction.* Springer, Berlin

Haken H, Portugali J. (1996). Synergetics, inter-representation networks and cognitive maps, in *The Construction of Cognitive Maps* Ed J Portugali. Springer Netherlands, Dordrecht

Helbing D, Farkas I, Molnar P, Bolay K. (2001). Self-organizing pedestrian movement. *Environment and Planning B.* **28**:361–383

Janssen-Jansen L. (2013). Delivering Urban Intensification Outcomes in a Context of Discontinuous Growth: Experiences from the Netherlands. *Built Environment* **39**(4):422–437

Karsenti E. (2008). Self-organization in cell biology: a brief history. *Nature Reviews Molecular Cell Biology.* **9**(3):255–262

Keller E. (2008). Organisms, Machines, and Thunderstorms: A History of Self-Organization, Part One. *Historical Studies in the Natural Sciences.* **38**(1):45–75

Keller E. (2009). Organisms, Machines, and Thunderstorms: A History of Self-Organization, Part Two. *Historical Studies in the Natural Sciences* **39**(1):1–31

Kendal J, Tehrani J, Odling-Smee F. (2011). Human niche construction in interdisciplinary focus. *Philosophical Transactions of the Royal Society B* **366**(1566):785–792

Kropf K. (2014). Ambiguity in the definition of built form. *Urban Morphology*. **18**(1):41–57

Kropf K. (2017). *The Handbook of Urban Morphology*. Wiley

Laland K. Brown G. (2006). Niche construction, human behavior, and the adaptive-lag hypothesis. *Evolutionary Anthropology*. **15**(3):95–104

Laland K, Odling-Smee F, Feldman M. (2001). Cultural niche construction and human evolution. *Journal of Evolutionary Biology*. **14**:22–33

Laland K, Odling-Smee F, Myles S. (2010). How culture shaped the human genome: bringing genetics and the human sciences together. *Nature Reviews Genetics*. **11**(2):137–148

Latty T, Beekman M. (2010). Food quality and the risk of light exposure affect patch-choice decisions in the slime mold *Physarum polycephalum*. *Ecology*. **91**(1):22–27

Le Corrbusier. (1947). *Concerning Town Planning*. The Architectural Press, London.

Lenton T, Daines S, Dyke J, Nicholson A, Wilkinson D, Williams H. (2018). Selection for Gaia across Multiple Scales. *Trends in Ecology & Evolution*. **33**(8):633–645

Lotka A. (1909). Contribution to the Theory of Periodic Reactions. *The Journal of Physical Chemistry*. **14**(3):271–274

Lotka A. (1925). *Elements of Physical Biology*. Williams and Wilkins, Baltimore

Mandelbrot B. (1982). *The fractal geometry of nature*. WH Freeman and Co, San Francisco

Marshall S. (2009). *Cities, design and evolution.* Routledge, Abingdon

Marshall S. (2012). Science, pseudo-science and urban design. *URBAN DESIGN International* **17**(4):257–271

Mehaffy M, Porta S, Rofè Y, Salingaros N. (2010). Urban nuclei and the geometry of streets: The ‘emergent neighborhoods’ model. *URBAN DESIGN International.* **15**(1):22–46

Mehmood A. (2010). On the History and Potentials of Evolutionary Metaphors in Urban Planning. *Planning Theory.* **9**(1):63–87

Moroni S. (2015). Complexity and the inherent limits of explanation and prediction: Urban codes for self-organising cities. *Planning Theory* **14**(3):248–267

Mumford L. (1938). *The Culture of Cities.* Harcourt, Brace and World Inc, New York

Mumford L. (1961). *The City in History. Its Origins, Its Transformations, and Its Prospects.* Harcourt, Brace and Company, San Diego

Murray J. (1988). How the Leopard Gets Its Spots. *Science.* **246**:614–621

Nientied P. (2016). Metaphor and urban studies-a crossover, theory and a case study of SS Rotterdam. *City, Territory and Architecture.* **3**(1):1–10

Odling-Smee F, Laland K, Feldman M. (2003). *Niche Construction: The neglected process in evolution*. Princeton University Press, Princeton

Pasquero C, Zaroukas E. (2016). Design prototype. in *Research Based Education 2016*. The Bartlett School of Architecture, UCL, London

Penn A, Turner J. (2018). Can we identify general architectural principles that impact the collective behaviour of both human and animal systems? *Philosophical Transactions of the Royal Society B.* **373**(1753):20180253–12

Portugali J. (1997). Self-organizing cities. *Futures.* **29**(4-5):353–380

Prigogine I, Nicolis G. (1967). On symmetry-breaking instabilities in dissipative systems. *The Journal of Chemical Physics.* **46**:3542

Rauws W, de Roo G. (2016). Adaptive planning: Generating conditions for urban adaptability. Lessons from Dutch organic development strategies. *Environment and Planning B.* **43**(6):1052–1074

Reid C, Latty T, Dussutour A, Beekman M. (2012). Slime mold uses an externalized spatial 'memory' to navigate in complex environments. *Proceedings of the National Academy of Sciences.* **109**(43):17490–17494

Rogers R. (1998). The Evolution of London. in *Evolution, Society, Science and the Universe* Ed A Fabian. Cambridge University Press, Cambridge

Rovira S. (2008). Metaphors of DNA: a review of the popularisation processes. *Journal of Science Communication.* **7**(1):1–8

Salingaros N. (2010). Complexity and Urban Coherence. *Journal of Urban Design.* **5**(3):291–316

Sharpe W, Wallock L. (1987). *Visions of the Modern City*. Johns Hopkins University Press., Baltimore

Silva P. (2016). Tactical urbanism: Towards an evolutionary cities approach? *Environment and Planning B.* **43**(6):1040–1051

Silvestro I. (2016). A metaphorical history of DNA patents. *RIFL.* **2**:49–63

Soria y Mata A. (1998). The linear city. in *Selected Essays.* Eds R Le Gates and F Stour. Routledge/Thoemmels Press, London

Steadman P. (2008). *The Evolution of Designs: Biological analogy in architecture and the applied arts - a revised edition.* Routledge, Abingdon

Tabony J. (2006). Historical and conceptual background of self-organization by reactive processes. *Biology of the Cell.* **98**(10):589–602

Tippett J. (2010). Going beyond the metaphor of the machine: complexity and participatory ecological design. in *A planner's encounter with complexity* Eds G de Roo and E Silva Ashgate, Farnham, Surrey

Turing A. (1952). The Chemical Basis of Morphogenesis. *Philosophical Transactions of the Royal Society B.* **237**(641):1–37

Turner J. (2004). Extended Phenotypes and Extended Organisms. *Biology and Philosophy* **19**:327–352

Turner J, Soar R. (2010). Beyond Biomimicry: What Termites Can Tell Us About Realizing the Living Building in *Industrialised, Integrated, Intelligent Sustainable Construction*. I3CON

Vanoutrive T, Damme I, Block G. (2016). On the Rationality of Network Development: The case of the Belgian motorway network. *17th IPSH Conference, Delft* **3**:235-246.

Vogel S. (1998). *Cat's Paws and Catapults*. Norton and Company, New York

Whittinghill L, Rowe D. (2011). The role of green roof technology in urban agriculture. *Renewable Agriculture and Food Systems.* **27**(04):314–322

Wiener N. (1948). *Cybernetics, or, Control and Communication in the Animal and the Machine.* MIT Press, Cambridge

Williams J. (2019). Circular Cities: Challenges to implementing looping actions. *Sustainability.* **11**(2):423

Wu N, Silva E. (2011). Urban DNA: Exploring the Biological Metaphor of Urban Evolution with DG-ABC Model. *AGILE.* 1-7

Yamu C, Frankhauser P, (2015). Spatial accessibility to amenities, natural areas and urban green spaces: using a multiscale, multifractal simulation model for managing urban sprawl. *Environment and Planning B.* **42**:1054-1078

Zhabotinsky A. (1964). Periodical oxidation of malonic acid in solution (a study of the Belousov reaction kinetics). *Biofizika.* **9**:306-311